

USE OF BIOACOUSTICS FOR POPULATION MONITORING IN THE
WESTERN SCREECH-OWL (*MEGASCOPS KENNICOTTII*)

by

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ABSTRACT

Recent studies suggest that individually distinctive vocalizations found in many avian species can be used in population monitoring. Vocal individuality of male Western Screech-Owls (*Megascops kennicottii*) was studied to determine its potential application as a long-term monitoring tool. As well, the male territorial call of this species was examined for regional and local dialects (variation in the territorial call structure). In total, recordings were collected at 46 territories between February and May, 2001 to 2003 from Vancouver Island and the south-central mainland of British Columbia. Radio-telemetry was used on two birds to confirm call stability between nights when re-recording the same individual at a known territory. As a quantitative descriptor of the calls, a total of 17 variables (3 frequency and 14 temporal) was measured from an average of 30 calls per individual. Discriminant function analysis of data from southern Vancouver Island indicated that vocal characteristics had low variability within individuals during a single breeding season, with 87.3% of calls correctly classified to an individual bird. Similar comparisons of calls recorded in two successive years suggested that these vocal signatures could be used to monitor territory re-occupancy between years. There was also a significant difference between vocalizations recorded at the regional scale, with 86.9% classification of calls to their geographic region of origin. Frequency measurements of calls were the key variables for distinguishing between regions. At the sub-regional scale, there appeared to be a gradient in call frequency characteristics from southeastern to northwestern Vancouver Island. Overall, results re-enforced the usefulness of bioacoustic research to conservation biology, in identifying and monitoring individuals, as well as providing insight into population dynamics (regional variation) for this species.

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1.0 GENERAL INTRODUCTION

Techniques that allow for quantitative, objective, and accurate population monitoring are a fundamental component of conservation biology. Population monitoring regularly requires identification of individual study animals to validate data collected on survival, long- and short-term movements, competition, behavioural strategies, and reproductive success (McGregor and Peake, 1998; McGregor *et al.*, 2000). Individual identification, however, often requires the use of invasive techniques (*e.g.*, mark-recapture methods, tagging or banding, and radio-telemetry), which may be undesirable for use with some sensitive species. Alternative techniques that use naturally occurring variation to identify individuals may, thus, prove useful. One such alternative involves the analysis of territorial vocalizations for individual recognition, which has been successfully applied to many avian species (McGregor and Dabelsteen, 1996; McGregor and Peake, 1998; McGregor *et al.*, 2000).

Both passerines and non-passerines often defend a breeding territory and attract a mate(s) through vocal behaviour (typically territorial songs) (Catchpole and Slater, 1995). As vocalizations are one of the primary modes of communication between most birds, individualistic cues inherent in vocal structure can be used by other birds to recognize and respond appropriately to specific signallers (*e.g.*, graded response to neighbours versus strangers); therefore, songs may be selected to be individually distinct (Falls, 1982; Catchpole and Slater, 1995; Lind *et al.*, 1996). As many population surveys rely on counts of vocalizing males, such individuality may provide a useful, non-invasive means of identifying individual birds.

Recording vocalizations during auditory surveys and later analysing them with spectrographic software has enabled researchers to use a combination of the singer's location and characteristics of the songs and/or calls (*i.e.*, frequency/pitch, duration and internote distance) to identify individuals (Galeotti *et al.*, 1993; Otter, 1996). This identification technique makes it possible to confirm detection of the same individual in subsequent site visits, allowing acquisition of detailed information on topics ranging from accurate population counts to site re-occupancy between breeding attempts (McGregor and Peake, 1998; McGregor *et al.*, 2000).

1.1 Benefits and Applications of Vocal Individuality

There are numerous benefits derived from identifying individual birds through their vocalizations (Galeotti, 1998; McGregor and Peake, 1998; McGregor *et al.*, 2000). First, by being able to identify individuals through vocalizations, such as territorial songs or calls, a larger number of individuals can often be monitored for some species than can be accomplished with other, more labour-intensive marking methods (McGregor and Peake, 1998). Although radio-telemetry and banding may provide higher (100%) confidence in individual re-identification, the potential to monitor a greater number of males efficiently and economically with song makes vocal "tagging" attractive, especially when individual variability is sufficient to approximate the same confidence of re-identification.

Second, vocal "tagging" is less invasive than other techniques and does not require capture and handling of the bird. This makes it preferable if the species is difficult to capture or sensitive to handling (McGregor and Peake, 1998). Tracking of individuals can also allow the identification of life-history characteristics, such as turnover rates in a population (Galeotti and Sacchi, 2001; Peake and McGregor, 2001). The use of vocal individuality as a

means of monitoring site fidelity, turnover rates, and annual survival estimates has provided an opportunity that would otherwise be difficult for many avian species. Identification of individuals can also provide increased accuracy during censuses within high-density regions, rather than merely assuming each singer is a distinct individual (McGregor and Byle, 1992; McGregor and Peake, 1998; Peake and McGregor, 2001). The use of vocal individuality to increase census accuracy, however, must be balanced against the extra time required for analysis. In combination with monitoring song rates of individuals, vocal behaviour can also provide a measure of condition, which may provide an indirect measure of habitat quality (Catchpole and Slater, 1995; Godfrey, 2003; Holschuh, 2004).

Finally, vocal monitoring of birds is relatively inexpensive, compared to marking individuals through radio-telemetry or other handling methods such as banding and colour marking (McGregor and Peake, 1998). One disadvantage at present, however, is that confirmation of an individual's identity is not done immediately in the field, but rather occurs through analysis of recordings at a later time. Despite this limitation, the advantages of the technique are making its use increasingly popular in long-term monitoring of vocal species that are otherwise difficult to monitor, such as owls.

1.2 Geographic Variation

Recordings collected to examine vocal individuality can also be analysed for geographic variation between populations. If distinct variations (dialects) exist, it may indicate patterns of reproductive isolation (Catchpole and Slater, 1995). Dialects are defined as a song tradition shared by members of a local population of birds, with macro- or microgeographic boundaries delineating one variant song tradition from another (Mundinger, 1982).

Macrogeographic variation represents changes in signal structure over a broad geographic

range, while microgeographic variation occurs between adjacent populations living under similar conditions; macro- and microgeographic variation are considered synonymous with the terms ‘regional dialects’ and ‘local dialects’ respectively (Mundinger, 1982; Galeotti *et al.*, 1996). Current research suggests that a combination of factors likely influence regional variation in acoustic structure and function, with no single explanation applying to all species (Date and Lemon, 1993; Ewert and Kroodsma, 1994; Miyasato and Baker, 1999; Baptista, 2000). Popular theories that may explain acoustic variation in song or complex call structure include: reproductive isolation, acoustic adaptation, life-history differences, and physiological influences (Catchpole and Slater, 1995; Miyasato and Baker, 1999). Below, I discuss each term.

The Genetic Adaptation Theory suggests that dialects act as population or group markers that through reproductive isolation help maintain genetic adaptations to local conditions (Miyasato and Baker, 1999). Variation in call structure may occur as a result of genetic drift in reproductively isolated groups, but the variability could become a reproductive isolating mechanism if it becomes beneficial for birds to mate within populations to favour the fixation of local adaptations (Thielcke, 1973; Naugler and Smith, 1991). This may be facilitated by females preferring to mate with males of the same dialect, which may lead to genetic isolation from other populations (Searcy and Yasukawa, 1996). Past or current geographical barriers may also influence the development of dialectal differences between populations, as they promote reproductive isolation (Martens, 1996).

According to the Acoustic Adaptation Hypothesis (AAH), also referred to as habitat matching, different habitat types select for variation in the structure of vocalizations such as

songs (Date and Lemon, 1993; Catchpole and Slater, 1995). For example, due to reverberation and song degradation that results from travelling through dense vegetation, birds that occupy dense vegetation should have songs of lower frequency (pitch) and few frequency fluctuations compared to birds occupying open habitat. This is because sound travels better at lower frequencies through dense habitat, and lower modulation is subject to less reverberation (Catchpole and Slater, 1995). Conversely, in open habitat, rapid modulations in amplitude (loudness) and frequency appear to transmit consistently and should be favoured by selection for acoustic structure (Brown and Handford, 2000). Much of the research conducted on geographic variation in passerine song structure has focused on its relationship to the AAH (Tubaro *et al.*, 1993; Tubaro and Segura, 1994).

Differences in life-history characteristics could also provide insight into why regional acoustic variation occurs in some avian species. For example, if song learning among juveniles extends beyond the period of natal dispersal young birds may use neighbouring males as song tutors post-settlement, thus perpetuating local dialects (Wilson *et al.*, 2000). Additionally, physiological influences such as size could result in geographic variation between populations (*i.e.*, larger birds are capable of producing lower frequencies).

As some of theories on geographic variation assume vocal learning, they may be less likely to explain variation in acoustic signals among species whose territorial calls are thought to be innate, such as owls (Konig *et al.*, 1999). Hypotheses that suggest variation may be attributable to genetic divergence of populations, however, are likely applicable to birds with innate vocalizations. As such, investigation of regional, as well as individual, variation could offer supplementary information in applied bioacoustic research for non-passerines.

Regional variation may provide insight into reproductive isolation among populations, while individuality may provide information on dynamics within populations. Acoustic monitoring may be especially useful in the study of birds that maintain their territories through singing, and for secretive and nocturnal species where visual marking is of limited value. Owls exhibit many of these characteristics and are therefore suitable candidates for bioacoustic research.

1.3 Monitoring Owl Populations

Despite the widespread occurrence of owls, and their importance as key predators, we still have a poor understanding of populations, demographics, habitat use, and the effects of habitat encroachment, in part due to their low detectability (Konig *et al.*, 1999; Takats *et al.*, 2001). Owls have several traits that result in low detectability, including nocturnal habits, low population densities in most areas, cryptic colouration, and the inconspicuous nature of the birds and their nests (Johnsgard, 1988). These traits introduce many challenges when attempting to inventory and monitor owl populations.

To overcome some of these obstacles, a number of inventory and research methodologies have been developed. Two of the most common methods for research on owls include radio-telemetry and call broadcast surveys. Radio-telemetry has been applied to obtain information on home range size, hunting behaviour, habitat selection, breeding chronology, and breeding behaviour; however, radio-telemetry is invasive, labour-intensive and costly, which can limit the number of individuals studied with this method. Call broadcast surveys are known to be effective in collecting information on distribution, relative abundance, and species diversity of many nocturnal owls (Resource Inventory Standards Committee, 1998; Takats *et al.*, 2001). One of the limitations with broadcast surveys is that they can be relatively inaccurate

because it is typically assumed that each detection is a separate individual (McGregor and Peake, 1998). More recently, vocal studies (bioacoustics) have been used in research on owls. A combination of broadcasting calls and recording the vocal responses may be applied to investigate vocal individuality, site turnover rates, geographic variation in vocal structure, and call rates in this phylogenetic group.

The application of vocal individuality to population monitoring of highly vocal owl species has demonstrated great potential as a useful conservation tool (Galeotti and Sacchi, 2001; Delport *et al.*, 2002). Vocal individuality has been demonstrated for a number of owl species including the Eastern Screech-Owl (*Megascops asio*) (Cavanagh and Ritchison, 1987), Tawny Owl (*Strix aluco*) (Galeotti and Pavan, 1991), Northern Saw-whet Owl (*Aegolius acadicus*) (Otter, 1996; Holschuh, 2004), and Eurasian Pygmy-Owl (*Glaucidium passerinum*) (Galeotti *et al.*, 1993) (see also Chapter 2). In these bioacoustic owl studies, a series of temporal and frequency variables were selected and measured for a number of calls from each individual to determine which variables provided a good indication of individual variation. Selection of variables and type of analysis can vary according to species and research objectives. For example, Galeotti *et al.* (1993) used qualitative and quantitative analyses of spectrograms of tape-recorded calls of male Eurasian Pygmy-Owls and found that a combination of three variables (fundamental frequency, duration of notes, and internote interval) allowed discrimination of individuals. Otter (1996) found that the frequency of calls explained the majority of variance among male Northern Saw-whet Owls, yet the inclusion of internote interval and note length was necessary to successfully discriminate all individuals. These studies demonstrated that variation existed within the territorial calls of

owls, which allowed for individual identification, and emphasized the importance of measuring both temporal and frequency variables for bioacoustic research.

Non-migratory, highly vocal species such as the Western Screech-Owl (*Megascops kennicottii*) provide a suitable test case for long-term monitoring through vocal behaviour. In addition, the taxonomy of this species is influenced by variation in the territorial call structure of different populations and subspecies (Konig *et al.*, 1999). Therefore, it is important to investigate geographic variation in call structure, and the potential conservation implications (Herting and Belthoff, 2001).

1.4 Focal Species - Western Screech-Owl

The Western Screech-Owl is a widespread species that occurs throughout much of western North America (Johnsgard, 1988). In Canada, it is found throughout coastal and southern British Columbia (B.C.) (Campbell *et al.*, 1990). Within B.C. there are currently two recognized subspecies. *M. k. kennicottii* on the coast and *M.k. macfarlanei* in south-central B.C. (Cannings and Angell, 2001).

A third subspecies from B.C., *M. k. saturatus*, was described by Brewster in 1891 as paler and smaller than *M. k. kennicottii* (Hekstra 1982). This taxon was restricted to southeastern Vancouver Island and the Gulf and San Juan Islands (Hekstra 1982). It was not recognized by the last full treatment of the subspecies of North American birds (AOU 1957), but was recognized by Hekstra (1982). Recent reviews of screech-owl taxonomy (Cannings and Angell, 2001; Gehlbach, 2003) found insufficient data to support the recognition of this subspecies. All coastal populations in B.C. are now treated as one subspecies (*M. k.*

kennicottii) due to the lack of literature supporting a distinct subspecies on Vancouver Island and the Gulf Islands (Conservation Data Centre of B.C., 2004).

1.4.1 Status

Historically, Western Screech-Owls are classified as locally abundant over parts of their range in B.C., although some populations are now believed to be in decline (Cannings and Angell, 2001; Fraser *et al.*, 1999). A recent review of the species by the Committee on the Status of Endangered Wildlife In Canada (COSEWIC) determined that the coastal subspecies was a population of ‘Special Concern’ (particularly sensitive to human activities or natural events but not endangered or threatened), while the interior subspecies was assessed as ‘Endangered’ (at risk of extirpation) (Chaundy-Smart, 2002). At the provincial level of government, portions of the coastal population are considered vulnerable to extirpation or extinction (Blue-listed), while the interior population of Western Screech-Owl is considered critically imperilled (Red-listed) (Conservation Data Centre of B.C., 2004).

Although widespread, populations are reported to be in decline in parts of B.C., likely due to large-scale forest harvesting at low elevations, agricultural development, urbanization, loss of snag trees, and likely predation by Barred Owls (*Strix varia*) (Fraser *et al.*, 1999; Chaundy-Smart, 2002; Conservation Data Centre of B.C., 2004). According to species specialists, little is known of current population demographics, and effects of nest cavity removal through land development and resource extraction, of either subspecies in B.C. (Fraser *et al.*, 1999).

1.4.2 Natural History

Western Screech-Owls in B.C. are considered non-migratory, with the pair remaining at the territory throughout the non-breeding season (Cannings and Angell, 2001). This species is

considered to be monogamous, retaining the same mate for life (Herting and Belthoff, 2001). Males start to actively re-establish territory boundaries through heightened singing behaviour from February to March, with breeding and egg laying occurring predominately in March and April (Cannings and Angell, 2001). Incubation takes three to four weeks (average of 26 days), with most young hatching from early May to the first week of June, then fledging 35 to 42 days later (Bent, 1938 cited in Campbell *et al.*, 1990). Brood size ranges from 1 to 5 young, with dispersal of first-year birds typically occurring in late summer to early fall (Cannings and Angell, 2001). Few detailed studies have been conducted on natal dispersal distances for this species. A study in southern Idaho indicated an average of 14.7 km based on data from 13 females, and 5.1 km based on data from 15 males (Ellsworth and Belthoff, 1997).

Western Screech-Owls are found in woodland habitats at lower elevations and are often associated with mixed deciduous/coniferous forests near riparian areas (Johnsgard, 1988; Cannings and Angell, 2001). In B.C., nests are usually found in cavities 1.2 to 12.2 m up a tree, mainly on sites located below 600 m in elevation (Campbell *et al.*, 1990). Nest trees have included a broad range of coniferous and deciduous species. Nest boxes, natural cavities, and those made by primary cavity nesters such as Pileated Woodpecker (*Dryocopus pileatus*) and Northern Flicker (*Colaptes auratus*) are used for nesting by Western Screech-Owls (Campbell *et al.*, 1990). At present, few detailed home range and territory size estimates have been determined for this species in North America (Johnsgard, 1988; Cannings and Angell, 2001). Research by Hayward (1983) in central Idaho indicated a home range of two radio-tagged birds to be 3-9 hectares (~0.20-0.34 km diameter), and 29-58 hectares (~3.27-6.54 km diameter) respectively. A study on Western Screech-Owls in

southern California calculated an average of 2.1 territories per kilometre of river channel, with a minimum average distance of 420 m between nest sites (14 territories spaced linearly along 6.4 km) (Feusier, 1989).

As with home range requirements, little is known about the specific diet of Western Screech-Owls in Canada. As a species, they have been reported to feed on a wide variety of prey including birds, small rodents, amphibians, reptiles, fish, insects, slugs, snails and worms (Johnsgard, 1988). Diet varies widely depending on location, and from year to year according to prey availability, with insects becoming an important part of the diet in the spring and summer (Cannings and Angell, 2001). Information on seasonal dietary requirements of the Canadian populations of this species would be helpful for conservation efforts.

1.5 Thesis Outline

1.5.1 Vocal Individuality and Long-term Monitoring

Numerous studies have demonstrated vocal individuality in birds, but few have applied the knowledge to long-term monitoring. Using discriminant function analysis, I examined whether the territorial advertisement call of male Western Screech-Owls was individually distinct enough to correctly classify (discriminate) individuals within and between years. Chapter 2 details my investigation of vocal individuality as a potential long-term monitoring tool for the Western Screech-Owl. The overall goal of this portion of the research was to provide a relatively non-invasive method for effectively studying and monitoring Western Screech-Owl populations in B.C., which would be used to augment long-term conservation of the species.

1.5.2 Macro- and Microgeographic Variation in the Territorial Call

All Screech-Owls (*Megascops*) are separated taxonomically to some degree by voice (Konig *et al.*, 1999). Presently eight subspecies of *Megascops kennicottii* are recognized in North America (Gehlbach, 2003). At one time, up to 18 subspecies of Western Screech-Owl were recognized, but these distinctions were primarily based on vocal and morphological descriptions from relatively few specimens (Hekstra, 1982; Johnsgard, 1988). It is now suspected that some of the variation in call characteristics relied on to assist in the classification of subspecies may actually be a result of individual variation (Konig *et al.*, 1999). In Chapter 3, I investigate regional variation using recordings of multiple males from the northern and southern Vancouver Island populations of the coastal subspecies (*M.k. kennicottii*) in comparison with the distinct subspecies in south-central B.C. (*M.k. macfarlanei*). The intent was to determine whether vocal divergence was as great within as between subspecies, partially to determine whether the recent grouping of the northern and southern races of the Vancouver Island population into a single subspecies (Conservation Data Centre of B.C., 2004) was warranted. To further clarify this, I also compared sub-regional variation among local populations of this species along Vancouver Island.

1.6 Study Area

Recordings were collected from southern (Victoria and Duncan), central (Campbell River), and northern (Nimpkish Valley) Vancouver Island, and the south-central mainland (Okanagan Valley) of British Columbia, Canada (Fig. 1.1). Elevations ranged from 50 to 450 m. The majority of detailed surveys for vocal individuality took place near Victoria and Duncan, located on southern Vancouver Island. In partnership with another study, birds near Campbell River (central Vancouver Island) were used for individual identification with

radio-telemetry (Doyle and Pendergast, unpublished data). Recordings were also collected from northern Vancouver Island and the south-central mainland for use in an analysis of variation in territorial call structure of Western Screech-Owls in British Columbia.

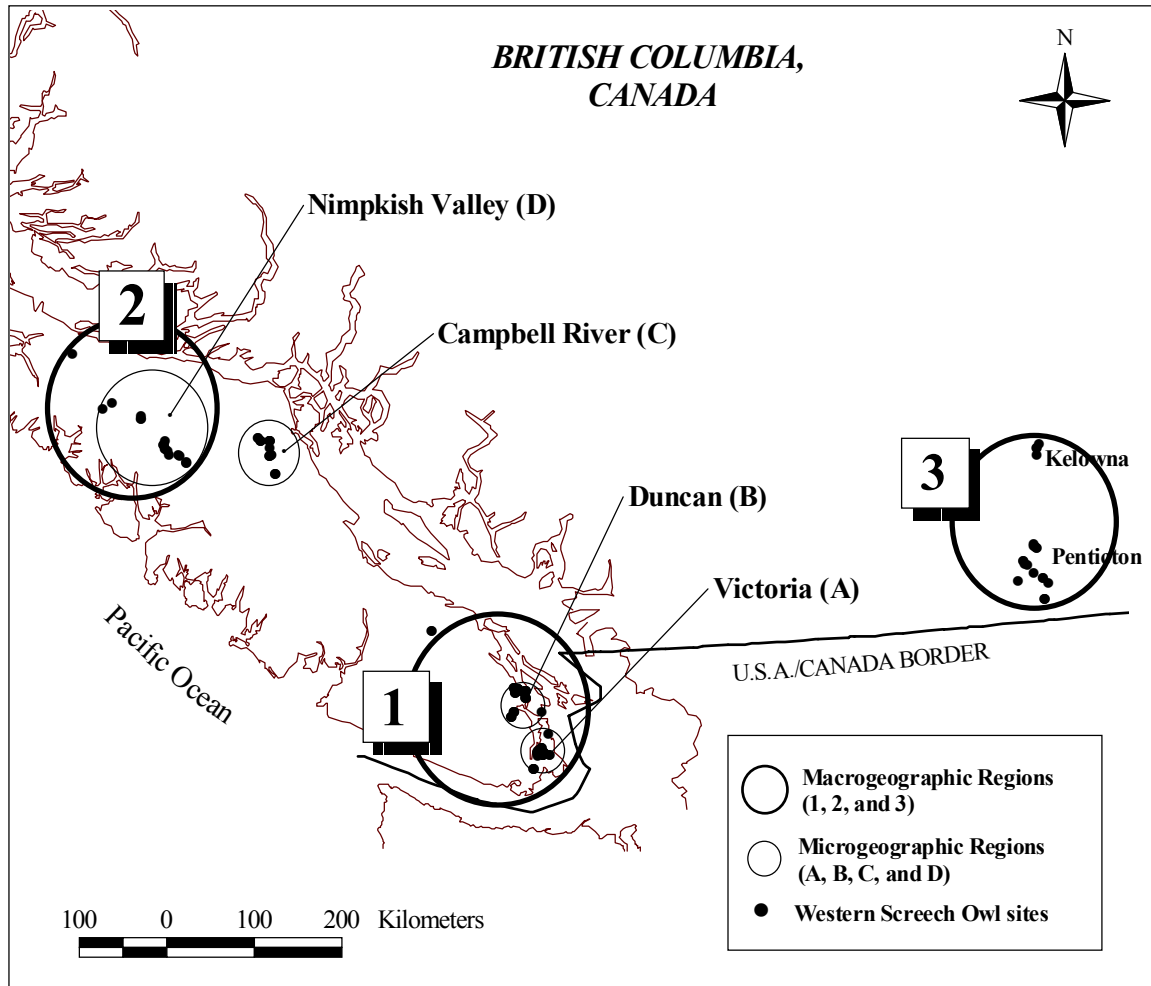


Fig. 1.1: Study area locations of Western Screech-Owl sampling between 2001 to 2003. Three distinct regions are shown in large circles: southern Vancouver Island (Region 1) and northern Vancouver Island (Region 2), representing the subspecies *Megascops kennicottii kennicottii*; and south-central mainland (Region 3) representing *M.k. macfarlanei*. In addition, four local (sub-region) populations were sampled along a southeast-to-northwest distribution of birds on Vancouver Island: Victoria (A), Duncan (B), Campbell River (C) and Nimpkish Valley (D).

1.6.1 Coastal British Columbia

Habitat on Vancouver Island was representative of northern hemisphere coastal rainforest, with varying levels of rural and urban development. Common tree species consisted of Western Hemlock (*Tsuga heterophylla*) and Western Redcedar (*Thuja plicata*), interspersed with Douglas-fir (*Pseudotsuga menziesii*), Broadleaf Maple (*Acer macrophyllum*), and Arbutus (*Arbutus menziesii*). Territories of Western Screech-Owls on southeastern Vancouver Island were located within the Coastal Douglas-fir biogeoclimatic zone, while the northern Vancouver Island sites were within the Coastal Western Hemlock biogeoclimatic zone (Meidinger and Pojar, 1991).

1.6.2 South-Central Mainland of British Columbia

As with Vancouver Island study areas, the south-central mainland sites were located within varying levels of rural and urban development. In contrast, habitat was representative of northern hemisphere open, dry forest, dominated by Ponderosa Pine (*Pinus ponderosa*) and Douglas-fir, with patches of Western Redcedar, Black Cottonwood (*Populus trichocarpa*), Trembling Aspen (*Populus tremuloides*), and Water Birch (*Betula occidentalis*) adjacent to riparian areas. South-central mainland territories of Western Screech-Owls were found within the Ponderosa Pine and Bunchgrass biogeoclimatic zones (Meidinger and Pojar, 1991).

1.7 Survey Effort

Call broadcast surveys took place over three seasons, with the initial year a pilot assessment for feasibility. Survey effort fluctuated between years due to differences in annual research priorities (Table 1.1). The first season (2001) focused on locating active territories, roost sites, and nests for reliable recordings and long-term monitoring. The second season (2002)

expanded the number of sites monitored for vocal individuality, and collected multiple recordings from each site within a single season. During the second season, I also collected recordings from the south-central mainland population (*M.k. macfarlanei*) for investigation of regional variation. During year three (2003), sites on southern Vancouver Island recorded in 2001 and 2002 were revisited. Recordings were also collected from the northern Vancouver Island population for regional comparison of territorial call structure.

Table 1.1: Western Screech-Owl call broadcast survey efforts 2001-2003. Number of males recorded each year is followed by the number of high quality, successful recordings in brackets.

Year	Survey Period	Number of Sites Surveyed	Number of Call Broadcast Surveys	Number of Detections	Number of Males Recorded	Number of Females Detected
2001	Feb. 3 rd to May 15 th	35	78	37	9 (8)	2
2002	Feb. 15 th to May 1 st	290	473	133	35 (31)	10
2003	Feb. 10 th to April 29 th	155	267	84	33 (29)	16
		Totals	818	254	77 (68)	28

During surveys from 2001-2003, Western Screech-Owls were detected during 254 of 818 (31%) surveys, with 13 observations of spontaneous calling and the remaining detections elicited via call broadcast. Females were detected at 44 (17%) of the 254 successful survey sites for Western Screech-Owls (Table 1.1). Sampling was not random, as approximately half of the sites surveyed were known territories.

Surveys typically started between 1700 h to 1900 h and ended from 0000 h to 0300 h. Time to detection ranged from <1 minute to a maximum of 44 minutes at a given site, averaging a six-minute response. Number of days between multiple, successful recording sessions at individual territories averaged 28 days in 2001 (range 6-90), 11 days in 2002 (range 2-54), and 27 days in 2003 (range 9-43). Other species detected during surveys from 2002-2003

included Northern Pygmy-Owl (*Glaucidium gnoma*) (n=1), Northern Saw-whet Owl (n=28), Barred Owl (n=35), Great Horned Owl (*Bubo virginianus*) (n=30), and Long-eared Owl (*Asio otus*) (n=2).

Despite heavy dependence on vocal surveys to inventory and monitor Western Screech-Owl populations, few studies have documented the vocal repertoire and behavioural contexts associated with the various call types for this species. Cannings and Angell (2001) note that a detailed cataloguing of the vocal repertoire of the species is required. Detailed studies of Western Screech-Owl vocal repertoires may assist in the identification of ideal call types for use in acoustic monitoring, as well as provide the basis for further investigation of other vocalizations. Vocal repertoire studies may also provide information about life-history traits that could be beneficial for conservation of the species (*e.g.*, pairing status, nest tree location, etc.). Due to the lack of information available on the vocal repertoire of Western Screech-Owls, I have included an overview of vocalizations that were detected in response to my primary research efforts on vocal individuality (Chapter 2) and regional variation in the territorial call (Chapter 3).

1.8 Vocal Repertoire of Western Screech-Owls

Western Screech-Owls primarily use vocalizations to maintain their territories, with call rates highest during the breeding season from February through May (Johnsgard, 1988; Cannings and Angell, 2001). Their vocal repertoire is dominated by two call types, the primary territorial ‘bouncing ball’ call, and the double trill call, both consisting of a series of single hoot notes. These call types are produced by both males and females. The following vocal descriptions refer to calls made in response to the broadcast of a conspecific adult male territorial call during the breeding season (February to May, 2001 to 2003) (see Chapter 2).

1.8.1 Primary Territorial Call (Bouncing Ball)

According to Johnsgard (1988), the primary ‘bouncing ball’ call consists of 12-15 notes for Western Screech-Owls along the Pacific Coast, with populations located further inland having shorter territorial calls of eight or nine notes, but sometimes as few as four. Notes typically became more closely spaced toward the end (resulting in the “bouncing ball” effect). Literature available on primary territorial call characteristics for this species shows variability among sexes and regions in a number of call measures (Table 1.2).

Table 1.2: Summary of the primary territorial call characteristics of Western Screech-Owls in North America. FMA indicates Frequency at Maximum Amplitude. Averages for frequency start and end, FMA, number of notes per call, and call length are provided \pm S.D. when available from the source.

Location	Sex	Number of birds	Start (Hz)	End (Hz)	FMA (Hz)	Number of notes/call	Call length (seconds)	Source
Arizona	M	1	635	615	-	10	1.4	Keller (1988)
Okanagan, B.C.	M	1	600	635	-	12	2.0	Neville (1996)
S. California	M	1	600	-	-	5-8	-	Feusier (1989)
	F	1	1000	-	-	-	-	
Idaho	M	15	-	-	602	9.0 \pm 0.4	1.5 \pm 0.1	Belthoff (2001)
	F	10	-	-	868	9.2 \pm 0.4	1.5 \pm 0.1	
Duncan, B.C.	M	13	672 \pm 21	675 \pm 53	697 \pm 20	11.3 \pm 2.7	1.8 \pm 0.2	Chapter 3 and Tripp (unpublished data)
	F	1	839 \pm 35	868 \pm 32	939 \pm 17	13.8 \pm 0.9	2.0 \pm 0.1	
Campbell River, B.C.	M	9	627 \pm 27	645 \pm 36	678 \pm 46	11.7 \pm 1.4	1.8 \pm 0.2	
	F	1	764 \pm 86	810 \pm 57	869 \pm 57	11.2 \pm 1.0	2.2 \pm 0.1	
Okanagan Valley, B.C.	M	10	593 \pm 32	603 \pm 36	634 \pm 41	11.4 \pm 1.7	1.8 \pm 0.2	
	F	1	676 \pm 34	788 \pm 35	841 \pm 22	16.5 \pm 1.5	2.7 \pm 0.2	

The territorial call structure appears to be suited for long-range communication (Konig *et al.*, 1999). As with other owls, its mean fundamental frequency is well below 1 kHz, and spacing of notes is likely ideal for transmission through dense, wooded vegetation (Catchpole and Slater, 1995). Western Screech-Owls have been observed calling back and forth to each other between territories over distances >500 m (pers. obs.). The primary territorial and the double trill calls have successfully been used as a non-invasive classification of sex, with

females having higher pitched calls than males (Herting and Belthoff, 2001) (Table 1.2). The difference between call structure in males and females likely aids in quick identification of the sex, to respond appropriately to intruders versus potential mates (Herting and Belthoff, 2001).

The primary territorial call was given more frequently than other call types by both sexes in response to call broadcast surveys in my study (Fig. 1.2).

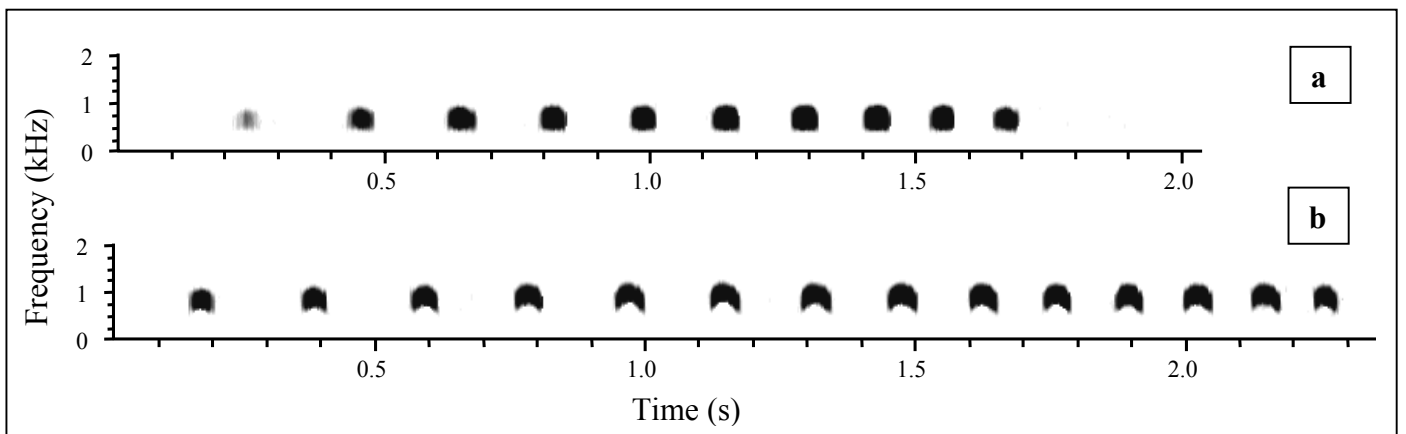


Fig. 1.2: Spectrogram examples of primary territorial ‘bouncing ball’ vocalizations given by Western Screech-Owls in response to call broadcast of a conspecific: a) male territorial call, and b) female territorial call.

Examples of this call type, recorded during my research, consisted of 11 hoot notes on average (range of 6-20 notes per call) for males. When call type and rates were calculated for each macrogeographic region surveyed, the territorial call was given >90% of the time (91% of 3,770 calls recorded on southern Vancouver Island, 95% of 947 calls recorded on northern Vancouver Island, and 94% of 847 calls recorded in south-central B.C.). Average call rate consisted of five territorial calls per minute throughout a given bout of calling (range of 1 to 12 per minute). Initial response to broadcasts had the highest call rates, gradually

slowing down over time to one and two calls per minute. For this study, I defined a bout of calling to be completed when greater than one minute of silence was observed between two successive territorial calls. Towards the end of a bout, a series of double trill calls were often recorded.

1.8.2 Double Trill Call

The second vocalization most frequently heard by observers from male and female Western Screech-Owls, in response to a territorial call broadcast, was the double trill. This call type consisted of a short series of notes (1-4) followed by a distinct gap of no sound, then a second, longer series of notes (Fig. 1.3).

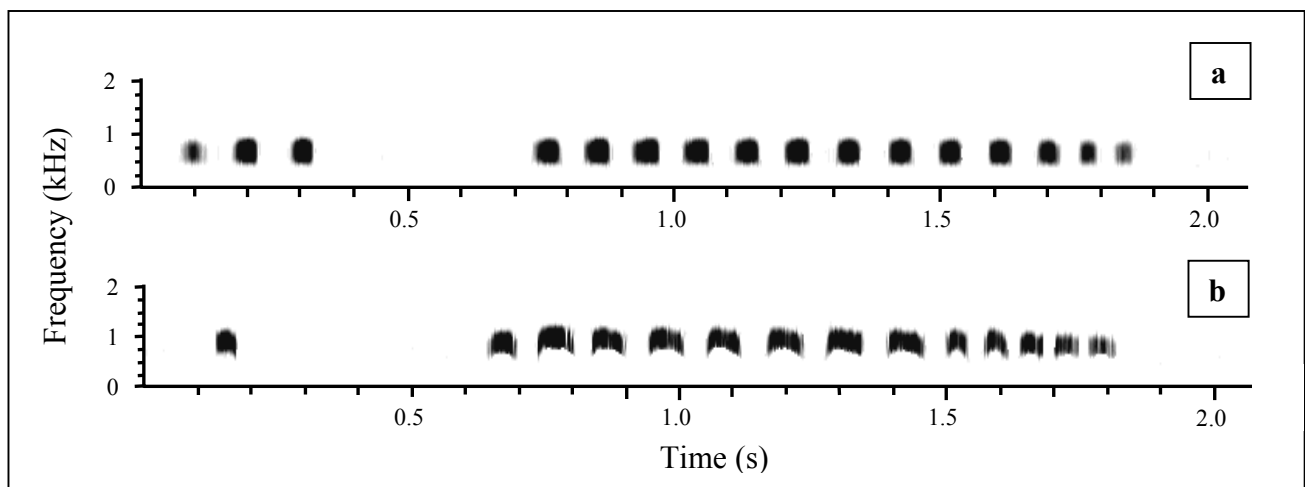


Fig. 1.3: Spectrogram examples of double trill vocalizations given by Western Screech-Owls in response to call broadcast of a conspecific: a) male double trill, and b) female double trill.

As with the territorial call, note spacing in the second half of the trill decreased towards the end. A slight variation in the call was sometimes heard when the bird dropped the first section of the trill. During my surveys this was typically encountered when the bird was

switching from the double trill back to the territorial call or *vice-versa* (transition call). Also, when this call was given at low amplitude, it was hard to hear the first part of the double trill. As this call was not heard often and tended to be relatively quiet compared to the territorial call, it may be more important in short-range communication. This call was described as the “contact call” by Johnsgard (1988).

Trills may also be given as an agitated response to broadcast of a conspecific, and have a territorial context (Johnsgard, 1988; Feusier, 1989). As these calls were given prior to copulation in at least three instances, they may represent periods of heightened levels of excitement in the birds, and may also be associated with copulation solicitation.

1.8.3 Drum Call

Another call type that was encountered during surveys has been described as the “drum call” by Cannings and Angell (2001). Figure 1.4 illustrates a two-second portion of a seven-second drum-call recorded during my surveys.

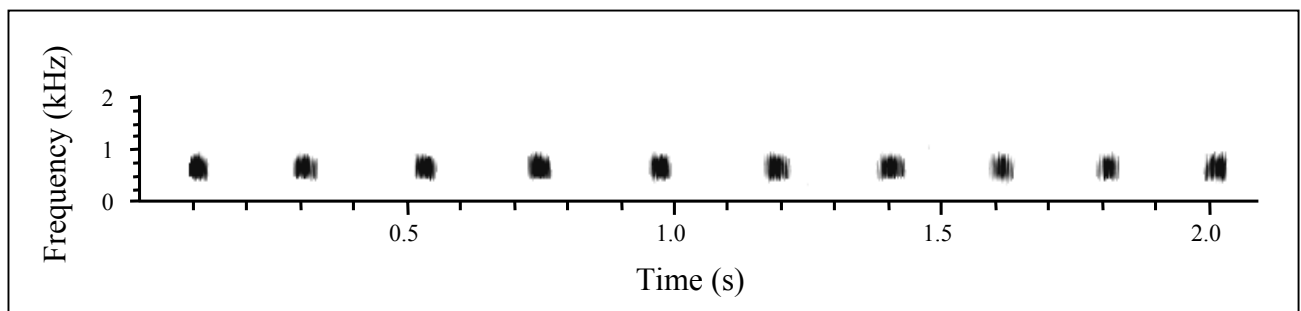


Fig. 1.4: Spectrogram example of a drum-call given by a male Western Screech-Owl in response to call broadcast of a conspecific.

During three years of detailed vocal observations, I detected this call only five times. Each occasion was in response to call broadcast of an intruding male at a known territory. This

call was heard before any other vocalizations, typically given softly, and then followed by the territorial call, which increased in volume with time. The drum call sounded similar to the beginning of a Northern Saw-whet Owl's territorial call, a series of evenly spaced, continuous notes. Feusier (1989) observed that the drum call was given by males at the nest tree early in the courtship period.

1.8.4 Female Two-Note and Single Note 'Yip' or 'Bark' Calls

Other call types detected during my call broadcast surveys included a single and two-note call given by females. They were always quiet, and often un-recordable even at very close range (< 15 m) (Fig. 1.5).

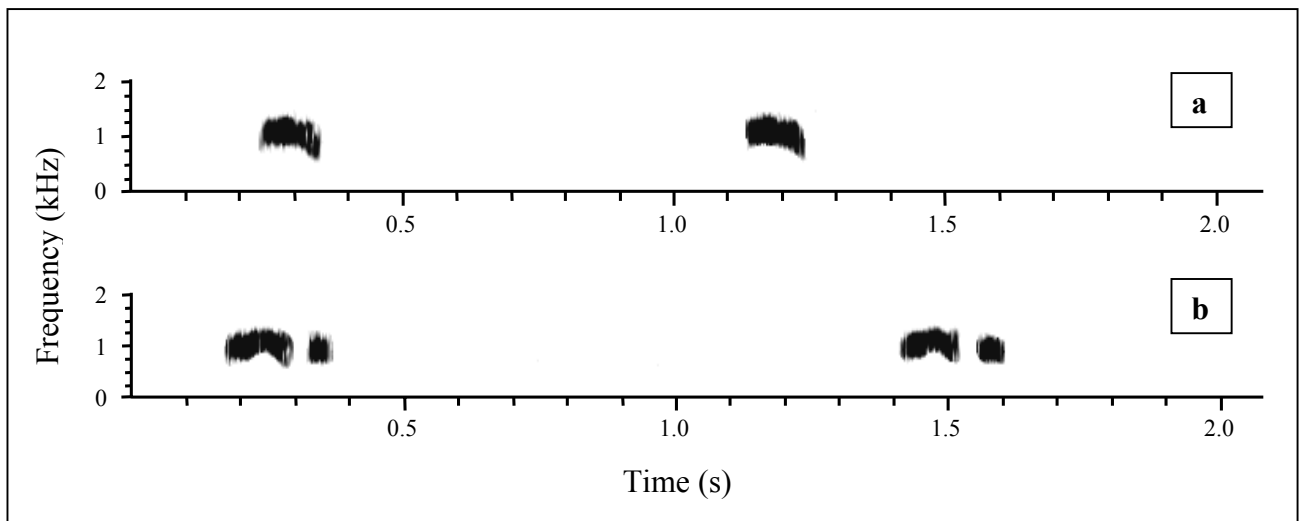


Fig. 1.5: Spectrogram examples of vocalizations given by female Western Screech-Owls in response to call broadcast of a male conspecific: a) female single note 'bark' call, b) female two-note 'begging' call.

Females were heard giving this contact or begging call while the male was performing the territorial and/or trill call, and following copulation. The two-note call may be similar to the

‘Chuckle-up’ call described by Cannings and Angell (2001). The single note call appeared to be used in the same context as the two-note call, and may be similar to the one described as the ‘yip’ in Johnsgard (1989). Females were heard giving the single, two-note, territorial and double trill calls during the breeding season (February and March), typically >30 minutes after initial call broadcast.

1.8.5 Male-Female Duets and Copulation

The primary territorial and the double trill calls have successfully been used as a non-invasive classification of sex, with females having higher pitched calls than males (Herting and Belthoff, 2001) (Table 1.2). The difference between call structure in males and females likely aids in quick identification of the sex, to respond appropriately to intruders versus potential mates (Herting and Belthoff, 2001). During surveys, male and female Western Screech-Owls were encountered after the call of a conspecific male was broadcast at a known territory, with male-female duets also observed (Fig. 1.6).

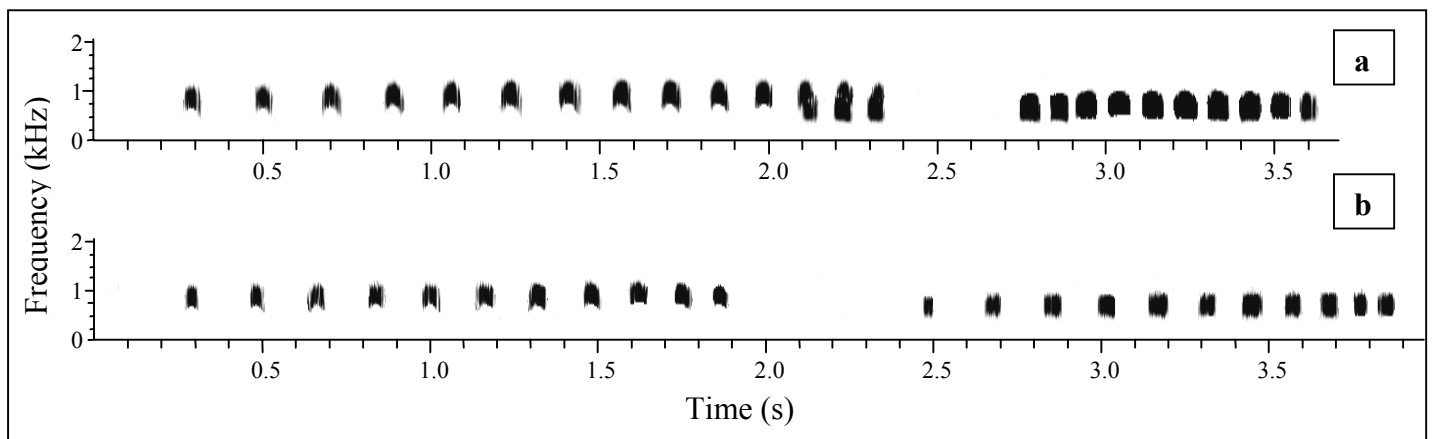


Fig. 1.6: Spectrogram examples of duets given by Western Screech-Owls in response to call broadcast of a conspecific: a) female territorial call overlapping with male double trill call, and b) female territorial call followed by male territorial call.

Male-female duets typically began with territorial calls from the male, followed by territorial or double trill calls from the female. Duets eventually led to copulation during my observations, with overlap of calls, increased calling rate (calls/minute), and a crescendo of heightened vocal activity (typically overlapping trill calls) followed by mounting of the female, with the male flapping its wings for balance. Actual copulation did not appear to last for more than a few seconds. During one occasion, a gentle, quavering blend of cr-r-oo-oo-oo-oo-oo notes was heard immediately following copulation (described in Johnsgard, 1989), but was too quiet to capture on the recording. Prior to and following copulation, a series of very quiet two-note calls was often heard from the female, while the male started a new bout of territorial calls.

Vocal courtship and display, followed by copulation, were visually observed on three separate occasions, just after dusk when ambient light was available. Subsequent breeding activity, however, was determined by ear (*i.e.*, once the breeding behaviour had been observed in association with a distinct series of vocalizations, it provided a baseline from which to assess breeding behaviour from subsequent audio detections). In total, copulation was noted on 12 separate occasions during surveys from 2001 to 2003, with three observations occurring in February, seven in March, and two in April.

1.8.6 Terminology - Songs and Calls

Terminology regarding classification of vocalizations is often confusing because of the gradients that can exist between songs and calls. Songs are traditionally defined as long, complex vocalizations produced primarily by males during the breeding season (Catchpole and Slater, 1995). They are usually long-range signals, and function in territorial advertisement and/or mate attraction. In contrast, calls are considered to consist of short,

simple vocalizations that are produced throughout the year. Calls are usually short-range signals that are produced equally by both sexes, and are used specifically in contexts other than those of song (Catchpole and Slater, 1995). For lack of better categorical descriptors for non-passerine vocalizations, in my study, the territorial and double trill of the Western Screech-Owl were defined as complex calls, with similar functions to those described above for songs.

2.0 VOCAL INDIVIDUALITY AS A POTENTIAL LONG-TERM MONITORING TOOL FOR WESTERN SCREECH-OWLS

2.1 Abstract

Recent studies suggest that individually distinctive vocalizations found in many avian species could be used in population monitoring. The focus of this study was to determine whether vocal identification of male Western Screech-Owls was possible, and if it could be applied as a long-term monitoring tool. Recordings were collected from 28 territories on southern and central Vancouver Island between February and May, 2001 to 2003. As a quantitative descriptor of the calls, a total of 17 variables (3 frequency and 14 temporal) were measured from each of 1,125 calls. Radio-telemetry was used on two birds to confirm that the same individual was recorded over successive sampling periods at a known territory. A discriminant function analysis resulted in 92.3% correct classification of 561 calls from one season of recording ($n = 28$ territories). Cross-validation of the model resulted in 87.3% correct classification. Variables that showed the greatest discriminant ability included length of call, internote distance between first and second note, and number of notes per call. Quantitative analysis of between-year recordings at known territories indicated that vocal signatures could be used to monitor re-occupancy. Of the 14 territories that had calls recorded in both years, four sites appeared to be occupied by a different owl in the second year (0-15% match in calls between years), while five sites had owl calls that were consistent between years (61-96%). The remaining territories had ambiguous classifications of 35-50% between years. My results indicated that the discriminant function analysis technique had a high reliability for identification of individual owls within a season, and sufficient ability to assist researchers in long-term monitoring of Western Screech-Owls.

2.2 Introduction

The use of avian vocalizations to identify individual birds has become a well-established research method for studying secretive non-passerines, including Corncrakes (*Crex crex*) (Peake *et al.*, 1998), Great Bitterns (*Botaurus stellaris*) (McGregor and Byle, 1992), African Wood Owls (*Strix woodfordii*) (Delpont *et al.*, 2002), Tawny Owls (*Strix aluco*) (Galeotti and Pavan, 1991; Appleby and Redpath, 1996), Pygmy-Owls (*Glaucidium passerinum*) (Galeotti *et al.*, 1993), and Northern Saw-whet Owls (*Aegolius acadicus*) (Otter, 1996). Results have shown that vocal signatures can provide a reliable means of identifying individuals of these species, with correct re-identification of individuals between observations (based solely on primary territorial songs or calls) often exceeding 80% accuracy.

One recent application of vocal individuality that has utility in avian conservation biology is the use of vocalizations to identify individuals over multiple years (long-term monitoring) (Peake *et al.*, 1998; Galeotti and Sacchi, 2001; Delpont *et al.*, 2002; Terry and McGregor., 2002). The use of vocal individuality as a means of monitoring site fidelity, turnover rates, and annual survival estimates has provided an opportunity that would otherwise be difficult for many species. This technique may be especially useful in studies of secretive or nocturnal birds where visual tags are of limited value and radio-telemetry can be limited by battery life and difficulty in catching individuals. The Western Screech-Owl (*Megascops kennicottii*) is such a species.

The Western Screech-Owl is a nocturnal, secretive, long-lived, non-migratory species that is fairly common throughout most of its range in the Pacific northwest coast of the U.S. and Canada (Cannings and Angell, 2001). Capture of individuals is fairly time-consuming, limiting the number of males available for telemetry studies. In addition, the small size of

the birds (<140 grams on average for males) (Gehlbach, 2003) precludes the use of transmitters that have battery lives greater than a few months; this requires multiple recaptures for long-term monitoring of site occupancy. These owls, however, are highly vocal, especially during the breeding season, and readily respond to call broadcast surveys (e.g., Hardy and Morrison, 2000; Cannings and Angell, 2001; Herting and Belthoff, 2001). The combination of these characteristics makes the Western Screech-Owl ideally suited for bioacoustic research. As little is known about current populations, basic life history, and effects of land development and resource extraction on Western Screech-Owls in Canada (Fraser *et al.*, 1999; Cannings and Angell, 2001; Chaundy-Smart, 2002), techniques that allow long-term monitoring of individuals and populations are essential for conservation of the species.

The primary objectives of this study were: 1) to determine the feasibility of individually identifying adult male Western Screech-Owls using territorial vocalizations within a single breeding season; and 2) to determine whether vocal individuality could be used to estimate turnover rates at known territories between seasons (long-term monitoring). To achieve these objectives, I repeatedly recorded the singing behaviour of multiple resident male owls on Vancouver Island over a single breeding season to compare within-season variability in call characteristics. I then returned to these sites over three successive breeding seasons and recorded the vocal activity of resident males to determine whether vocalizations remained stable between years at the same territories.

2.3 Methods

2.3.1 Study Area

Recordings were collected from southern (Victoria and Duncan) and central (Campbell River) Vancouver Island, British Columbia, Canada (48° N 123° W). Habitat was representative of northern hemisphere coastal rainforest, with varying levels of urban and rural development. Elevations ranged from 50 to 450 m. Censusing for Western Screech-Owls in this region has been conducted since 1999 (L. Darling, J. Hobbs, T. Tripp, unpublished data), though recording of males was not initiated until 2001.

2.3.2 Territorial Calls, Recording Methods and Spectrographic Analysis

The territorial call was selected for analysis because it was the most frequently heard vocalization from this species in response to a conspecific broadcast (Section 1.8.1). A total of 17 variables was measured for each territorial call that included number of notes per call (R1), call speed (a ratio of the second internote distance (*i.e.*, D3) to the penultimate note (*i.e.*, D6) measured, R2), number of notes per second (R3), total length of call in milliseconds (D1), six internote distance measurements (D2-D7), four note length measurements (N1-N4), average frequency at start of call (F1), average frequency at end of call (F2), and frequency at peak amplitude of call (F3) (measured in Hz) (Fig. 2.1). Variables included in the analysis were typical of those measured in other vocal individuality studies of non-passerines. To capture one of the common call characteristics of the Western Screech-Owl primary territorial call, R2 was included to provide the greatest contrast of distance between notes at the start and finish of the call. I chose the 2nd and penultimate internote distances, rather than the first and last, to improve accuracy; the first, and sometimes last notes, of the call are often quieter than the remaining notes, and as such can be subject to loss or degradation in more distant recordings.

A Marantz PMD430 cassette recorder (Marantz, Scarborough, Ontario), and Sennheiser MKH70 or ME 67 microphone (Sennheiser, Pointe Claire, Quebec) were used to collect recordings during the breeding seasons (mid-February to mid-May each year) from 2001 to 2003. Recordings were collected between 1700 h to 0300 h, during optimal conditions (low wind, no rain).

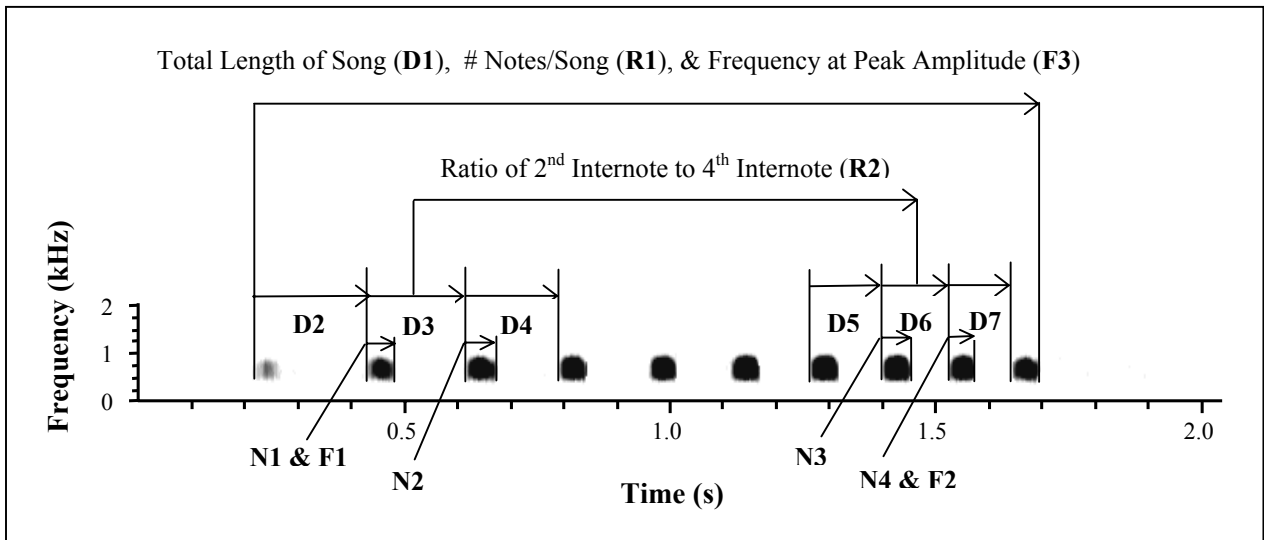


Fig. 2.1: Spectrogram of a Western Screech-Owl primary territorial call with variables measured for vocal individuality: D1 (Total length of call), D2-D7 (Internote distances), N1-N4 (Note length 1-4), R1 (Number of notes per call), R2 (Ratio D3/D6), and R3 (Number of notes per second – not shown). Frequency measurements included F1 (Mean frequency of second note), F2 (Mean frequency of second to last note), and F3 (Frequency at peak amplitude) (measured in kHz).

Initial surveys were conducted each year to confirm the presence of calling males at each of the known territory sites. A standardized call broadcast was used to elicit a response from territorial males. The broadcast consisted of five territorial calls of a conspecific, evenly spaced over one minute, followed by a two-minute listening period. This procedure was repeated up to three times for a total of three minutes of broadcast (15 calls). If a bird was

detected, broadcast was stopped after the one-minute interval was complete. A minimum of 15 minutes was spent at each site to maximize the likelihood of detection. Sex of the responding owl was determined based on clearly distinguishable audio difference in pitch between males and females; on average, female calls are 100-200 Hz higher than those of males and the range of the calls does not overlap between sexes (Section 1.8 and Table 1.2).

Male Western Screech-Owls are known to occupy their territories year-round (non-migratory) (Cannings and Angell, 2001), therefore, it was assumed that once a territory was located, the same male would occupy it for at least a single season. I was confident that I had recorded the same male within and between nights at the same site within a season due to: 1) repeated presence of a calling bird at the same location, generally within 100 metres of previous calling locations, 2) identification of nest and/or roost trees, 3) distance between recording sites likely exceeded the average territory diameter for the species (recording sites were separated by $\bar{x} = 2.92$ km, ranging from 0.90 to 8.42 km - by comparison the average inter-territory distance in an intensively surveyed area of southern Vancouver Island was 1.33 km (n = 11 territories) (Appendix 1)), 4) low likelihood of changes in territory occupancy (turnover) within a season based on banded population studies (J. Belthoff pers. comm.), and 5) unique vocal characteristics among some males that could be easily distinguished by the observer (*e.g.*, presence of unusual syllables in the call). As part of a separate study on Vancouver Island, two male Western Screech-Owls captured in 2003 were monitored via back-pack mounted radio-transmitters over a single breeding season. Subsequent relocations confirmed that both males remained within the same area as they had been captured (Doyle and Pendergast, unpublished data), thereby lending support to my assumption that the same bird occupied the same territory within a breeding season.

To account for potential seasonal variation in territorial call structure, I attempted to record males at each known territory on multiple occasions within a single season (2001: average = 2.25 recording nights per territory, range 1-6, $n = 8$; 2002: average = 2.81 recording nights per territory, range 1-8, $n = 22$; 2003: average = 1.63 recording nights per territory, range 1-6, $n = 22$). Overall, 13 of the 28 sites used for the vocal individuality analysis were recorded more than once within a single season (2001-2003: average = 2.17 recording nights per territory, range 1-6, $n = 28$). The two radio-tagged males were among this group, and were recorded on at least two nights to compare vocalizations from known individuals for seasonal variation.

Recordings were reviewed for high-quality calls from each territory (low background noise, and high sound intensity, typically <25 m from the bird). The territorial calls were then digitized for vocal individuality analysis using Avisoft SAS-Lab Pro software, Version 2.6 (Specht, 1993). To reduce background noise, calls were filtered above 1000 Hz and below 300 Hz for all individuals, thus avoiding the actual call frequency range of males (400-750 Hz). Variables were measured on screen using spectrogram parameters for frequency variables set at a resolution of 20 Hz, Fast-Fourier Transform (FFT) Length of 512 (used to digitize the signal to emulate a sine wave), bandwidth of 56 Hz, and temporal resolution of 2.9 ms (narrow setting). Temporal variables were measured using the wide bandwidth setting (324 Hz).

2.4 Analysis

2.4.1 Vocal Individuality Within A Season

To investigate within-season vocal individuality in Western Screech-Owls, a forward stepwise discriminant function analysis (DFA) (p to enter = 0.05) was conducted on the variables measured from each male's call using Statistica 6.0 (StatSoft, 2002).. A general lack of model cross-validation has been considered to be a weak point in previous vocal individuality DFAs (Terry *et al.*, 2001). I addressed this issue by using two datasets, one subset of calls from all individuals to build the model (learning set) and another subset to test it (test set).

Within the DFA, all 17 territorial call variables were assessed for their ability to correctly classify individuals to their territory of origin. The DFA selected the most significant variables and added them sequentially until it determined that adding extra variables did not result in significantly better discrimination (Manly, 1994; Quinn and Keough, 2002).

Variables that were highly correlated and did not provide additive variability were excluded from the resultant model (StatSoft, 2002).

Calls were randomly selected for analysis from high quality recordings (<25 metres of the observer, low wind, and no rain). A sample size of 30 calls per site was selected for analysis based on previous bioacoustic research (*e.g.*, Galeotti *et al.* (1993) \bar{x} = 19.5 calls per male (range of 10-35 calls for each of ten Pygmy-Owls); Galeotti and Pavan (1991) \bar{x} = 8 calls (range of 4-30 calls from each of 17 Tawny Owls); Cavanagh and Ritchison (1987) \bar{x} = 20.5 (range 7-30 calls from each of 24 Eastern Screech-Owls)). I aimed for the larger sample size of 30 calls per bird in order to provide enough cases to develop a learning set for the model, and a test set for cross-validation of the model. An average of 29.9 territorial calls (range 28-

30) per site ($n = 28$ birds in total), representing a single season of recording, was included in this analysis for a total of 837 territorial calls.

A subset of the calls (561 in total, 18-20 per site) was used in the learning set to derive the discriminant model. Where possible, the learning set included calls recorded at the same territory from different nights within the same breeding season. The use of calls from different nights and bouts of recording was intended to account for potential variability that might exist within an individual's call throughout the breeding season. A bout of calling was defined as complete when greater than one minute of silence was observed between two successive territorial calls.

As less than half of the territories in my sample were recorded only once ($n = 15$), the ability of a discriminant model to correctly identify calls collected at those sites may be somewhat biased because seasonal variation would not be included in the model. To test whether the difference in number of nights of recording per territory affected classification results within a single season, I conducted two DFAs, one on territories with multiple nights of recordings ($n = 13$ birds, 390 call samples, $\bar{x} = 30$ calls per site), and a second on territories with a single night of recording ($n = 15$ birds, 447 call samples, $\bar{x} = 29$ calls per site). F-to-enter was increased to 5.0 to reflect the reduced number of territories in the analysis (smaller sample size) in relation to number of variables ($p = 0.05$).

For territories that had multiple recordings ($\bar{x} = 3.61$, range of 2-6 nights of recording per site) within a single breeding season, calls from a different recording night, not included in the learning set, were used to test the model. This enabled me to examine whether call structure of birds from territories with multiple recording nights in the model were easier to

re-identify (higher correct classifications) than birds from territories with only a single recording sample. It also provided a means by which to test whether calls recorded on a different day, week, or month, varied enough to affect the overall discriminant ability of the model for a given territory.

For sites that were only recorded once, an average of 20 calls were randomly selected for use in the learning set. The remaining third of the cases was used as a test set (9-10 calls per site, for a total of 276). The use of a test set lends support to the ability of the model to accurately classify individuals, as none of the test calls were included in the learning set that derived the discriminant equation. Following the two DFA's, a regression analysis was conducted to determine if there was a relationship between the number of nights of recording included in the DFA model and the percent classification that resulted. A regression analysis was also conducted to test for percent correct classification in relation to the number of bouts included in the DFA model (*i.e.*, did the number of calling bouts recorded in a given night influence classification of calls from that territory in the DFA model).

2.4.2 Re-Identification Among Seasons

Based on the vocal individuality analysis within a season, I predicted *a priori* that $\geq 60\%$ call classifications between years were likely to represent the same individual occupying the same territory. As 60% was the lowest correct classification among territories in the cross-validation test sets within-year (see below), I considered $\geq 60\%$ to be a reasonable threshold criterion for re-identification between breeding seasons (years), as it would allow for minor variation across years in call structure. If variation is high enough for individuation of calls, however, the calls of two different individuals at the same territory should randomly cross-assign at low rates. To test this theory, 28 sites were randomly cross-assigned creating 14

sites in a learning set and 14 different sites as a test set. This control test was conducted twice for a total of 28 different territory combinations (*i.e.*, to mimic the 28 sites used in the DFA used to establish the upper threshold). As 26 of 28 (93%) of the control cases classified at $\leq 30\%$ in the DFA, I predicted that territories with classifications $\leq 30\%$ between years likely represent a new individual occupying the site.

A forward stepwise DFA was used to investigate whether vocal identification of individuals could be applied to determine territory turnover between years. Fourteen territories were successfully recorded over more than one breeding season. Data from the larger sample size year were used as the learning set to derive the discriminant model (28-30 calls per individual, 408 in total), and were typically recorded in 2001 or 2002. Calls recorded from a second year were used to test the model. An additional 288 calls (average = 20.85 per individual, range 15-30) were measured from a second year of recording to build the test set. In three cases, between-year comparisons were not in chronological order (Site 1, 7, and 21). For example, in 2002 Site 1 had a sample size of 21 calls, but in 2003 a larger sample size of 30 calls was obtained, therefore, year 2003 was used as 'year 1' in the model, and 2002 was 'year 2' test set. If calls were stable between years, then returning males should have had relatively high correct classification between breeding seasons.

Twelve additional territories were included in this analysis as a form of control to test the classification performance of the model for sites that were known to contain different birds between years. Including control cases in the between-year DFA analysis had two functions: 1) it demonstrated that two randomly assigned territories would have low cross-classification, confirming the ability of the model to recognize individual territory occupants that differed

between years; and 2) it demonstrated the average cross-classification of two individuals known to differ, which could then be used for defining a threshold for cross-classification in the true test sample. The control set was created by randomly selecting twelve territories not already used in the cross-year comparisons, and then randomly assigning two territories to each other. This design created six known false matches between years. I then proceeded to run a forward stepwise DFA ($n = 20$ sites, F-to-enter 1.0, $p = 0.05$).

2.5 Results

2.5.1 Accounting for Seasonal Variation

The discriminant analysis conducted on owls with multiple recordings within a single breeding season resulted in 95.8% (range of 75-100%) correct classification of calls included in the learning set to develop the model. Cross-validation of the model with the test set resulted in a correct classification of 87.3% (range of 60-100%) of the cases. Four variables (frequency at start of call (F1), and three measures of note length (N2, N3, and N4)) failed to enter the model following forward stepwise analysis. Similar DFA results occurred in a separate analysis for single recording sample sites, with a high correct classification of 96.3% (range of 75-100%) for the learning set, and 91.8% (range of 70-100%) for the test set. Three variables relating to note length (N1, N3), and internote distance (D4) failed to enter the model due to low discriminant ability.

Results of the regression analyses indicated no relationship between the number of nights of recording and correct classification rates of individuals for either the learning ($r^2 = 0.045$, $p = 0.278$) or test sets ($r^2 = 0.002$, $p = 0.792$). The regression analysis for percent correct classification in relation to the number of bouts included in the DFA also resulted in no significant relationship ($r^2 = 0.061$, $p = 0.202$ for learning set; $r^2 = 0.078$, $p = 0.149$ for test

set). As there appeared to be no effect of the number of nights over which recordings were collected on percent correct classification, the two datasets were combined for the final within-season DFA.

2.5.2 Vocal Individuality Within A Season

The final discriminant function analysis was conducted for all individuals ($n = 28$ individuals, 837 calls in total, F-to-enter set at 1.0, $p = 0.05$, 17 variables). Of the 28 sites included in the analysis, the model was able to correctly classify 92.3% of the 561 calls contained within the learning set (ranging from 75 to 100%) to the site of origin (Table 2.1).

The cross-validation resulted in a slightly lower classification of 87.3% of 276 calls contained in the test set (ranging from 60 to 100%) correctly assigned to the site of recording. For the two males with radio-transmitters, a classification of 95% and 100% occurred for the learning set (recordings from night 1) (Table 2.1). In the test set both sites performed at 80% (all test set cases were from a second night of recording). The four measures of note length (N1-N4), and the mean frequency at end of call (F2) had the lowest discriminant ability (F values of 3.47 to 5.38, Table 2.2).

Table 2.1: Results of within-year discriminant function analysis for vocal individuality in the male Western Screech-Owl territorial call within a single breeding season on southern Vancouver Island ($n = 28$). * indicate sites with radio-telemetry confirmation of individual identification during recording.

Site #	Year	#Days/ #Bouts	# Calls Sampled	% Correct Classified (Learning Set)	% Correct Classified (Test-Set)
1	2003	4/4	30	95.0	100.0
2	2002	3/6	30	100.0	60.0
3	2002	4/6	30	100.0	80.0
4	2001	2/3	30	95.0	100.0
5	2002	1/5	30	75.0	80.0
6	2002	1/2	29	100.0	77.8
7	2003	1/1	30	100.0	90.0
8	2002	1/1	30	75.0	70.0
9	2001	1/1	30	85.0	80.0
10	2001	1/3	30	100.0	90.0
11	2002	1/1	30	100.0	100.0
12	2002	1/3	30	100.0	100.0
13*	2003	2/3	30	95.0	80.0
14*	2003	2/5	30	100.0	80.0
15	2003	1/2	30	95.0	100.0
16	2002	1/3	30	100.0	100.0
17	2002	6/12	30	75.0	60.0
18	2002	6/8	30	80.0	100.0
19	2002	5/6	30	100.0	100.0
20	2003	1/2	30	95.0	70.0
21	2001	6/6	30	95.0	100.0
22	2002	2/2	30	85.0	70.0
23	2002	2/2	30	90.0	90.0
24	2001	1/1	28	90.0	100.0
25	2003	1/1	30	100.0	100.0
26	2001	3/3	30	75.0	80.0
27	2001	1/2	30	90.0	90.0
28	2003	1/1	30	95.0	100.0
Totals		61/93	837		
		2.2/3.3	29.9	92.3%	87.3%

Table 2.2: F-to-enter values of variables included in the discriminant function model for vocal individuality in the male Western Screech-Owl territorial call within a single breeding season on southern Vancouver Island ($n = 28$, F-to-enter 1.0, $p = 0.05$, 17 variables entered, degrees of freedom = 27). F values are listed in order of greatest to least discriminant ability in the model.

Variable	F-to-Enter	p-values
D1 (Total length of call)	39.83	<0.001
R1 (# notes/call)	39.58	<0.001
D2 (Internote distance between note #1 and #2)	28.28	<0.001
R2 (Ratio of 2 nd Internote to 4 th Internote Measure)	24.97	<0.001
D4 (Internote distance between note #3 and #4)	22.40	<0.001
R3 (#notes/second)	17.61	<0.001
D3 (Internote distance between note #2 and #3)	15.29	<0.001
D6 (Internote distance between third from last note and second from last note)	15.20	<0.001
F3 (Frequency at peak amplitude)	12.13	<0.001
F1 (Mean frequency at start of call, note #2)	9.74	<0.001
D5 (Internote distance between fourth from last note and third from last note)	8.20	<0.001
D7 (Internote distance between last two notes)	7.54	<0.001
N1 (Length of second note)	5.38	<0.001
F2 (Mean frequency at end of call)	4.90	<0.001
N4 (Note length of second from last note)	4.86	<0.001
N3 (Note length of third from last note)	3.52	<0.001
N2 (Note length of third note)	3.47	<0.001

2.5.3 Re-Identification Among Seasons

The discriminant model for the first year of recordings correctly classified 88.8% of the calls to their territory of origin. Recordings collected from the same territories in year two had a similar level of discrimination within a single season (90.7% correct classification) (Table 2.3).

Table 2.3: Results of discriminant function analysis for vocal individuality between years in the male, Western Screech-Owl territorial call on southern Vancouver Island ($n = 20$). * indicate the test cases, which were known to be different site locations and individuals between years.

Discriminant Model (Year 1)					Test Set (Second Year)						
Site #	Year	#Days/# Bouts	# of calls	% Correct Classified Year 1	Site #	Year	#Days/#Bouts	# of calls	% Correct Classified Year 2	% Correct Between Years	Turnover
1	2003	4/4	30	96.7	1	2002	1/1	21	95.2	61.9	No
2	2002	3/6	30	86.7	2	2003	1/1	20	85.0	50.0	?
3	2002	4/6	30	83.3	3	2003	2/2	20	95.0	75.0	No
4	2001	2/3	30	100.0	4	2002	4/6	30	100.0	86.7	No
5	2002	1/5	30	86.7	5	2003	3/3	20	85.0	15.0	Yes
7	2003	1/1	30	100.0	7	2002	1/5	19	100.0	0.0	Yes
8	2002	1/1	30	73.3	8	2003	4/4	20	85.0	15.0	Yes
9	2001	1/1	30	86.7	9	2003	1/1	20	55.0	40.0	?
17	2002	6/12	30	80.0	17	2003	1/1	15	100.0	73.3	No
18	2002	6/8	30	100.0	18	2003	2/2	20	90.0	35.0	?
20	2003	1/2	30	83.3	20	2002	1/1	15	93.3	53.3	?
21	2002	6/6	30	83.3	21	2003	2/2	20	90.0	35.0	?
22	2002	2/2	30	86.7	22	2003	1/1	20	100.0	0.0	Yes
24	2001	1/1	28	96.4	24	2003	1/1	28	96.4	96.4	No
<i>n</i>		39/58	418				25/31	288			
\bar{x}		2.7/4.1	29.9	88.8			1.7/2.2	20.6	90.7	45.5	
*11	2002	1/1	30	96.7	*10	2001	1/2	20	95.0	0.0	
*12	2002	1/3	30	100.0	*25	2003	1/1	20	95.0	0.0	
*15	2003	1/2	30	96.7	*16	2002	1/3	20	95.0	0.0	
*27	2001	1/2	30	96.7	*13	2003	2/2	20	95.0	0.0	
*28	2003	1/1	30	100.0	*14	2003	2/3	20	95.0	0.0	
*6	2002	1/2	29	96.6	*23	2002	2/2	20	100.0	0.0	
<i>n</i>		6/11	179				9/13	120			
\bar{x}		1.0/1.8	29.8	97.8			1.5/2.1	20	95.8	0%	

Use of one year of calls as the DFA learning set, and a second year of calls from the same territories as the test set, resulted in only 45.5% of calls correctly classified to their territory of origin (Table 2.3 and Fig. 2.2). Four test sites also indicated potential turnover between years, based on call classifications of 0-15%, which was well below the pre-set limit of $\leq 30\%$ cross-classification. In contrast, high call classification at five additional sites suggested that the same bird was present between years (61.9 to 96.4% call classification between years). Results for the remaining five sites were ambiguous: Site 2 (50%), Site 9 (40%), Sites 18 and 21 (35%), and Site 20 (53.3%) (Table 2.3 and Fig. 2.3).

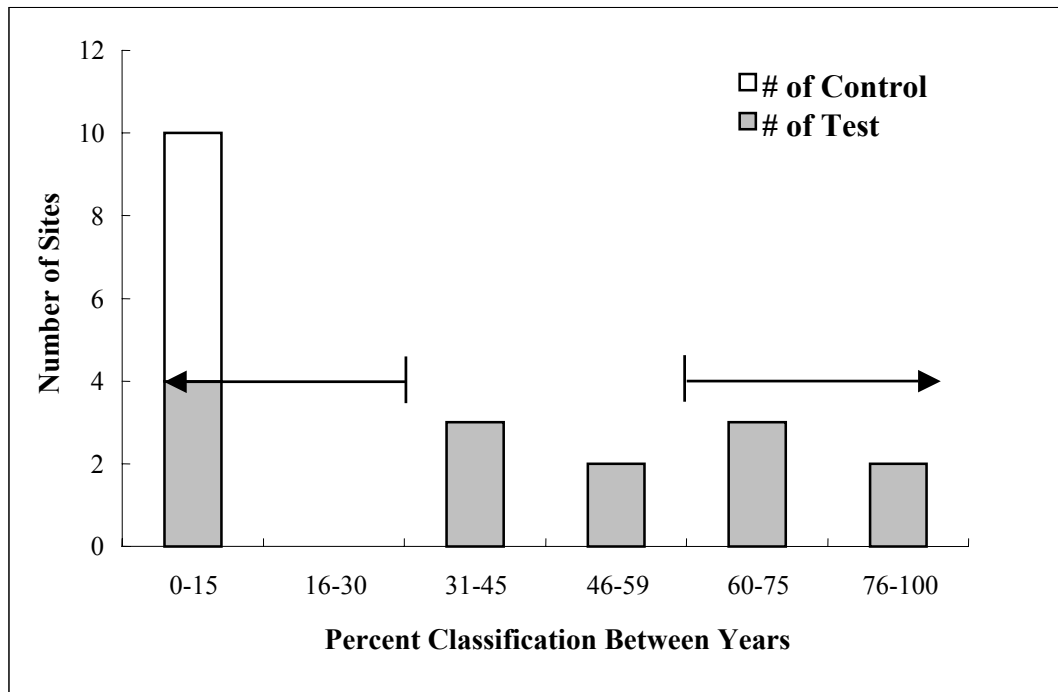


Fig. 2.2: Distribution of classification of calls between years for male Western Screech-Owl territories on southern Vancouver Island. “Re-occupancy” was assigned where $\geq 60\%$ of calls recorded in the second year were classified to the same territory recorded in the first year (arrow to the right). Indication of potential turnover was considered when $\leq 30\%$ of the calls were classified to the same territory (arrow to the left). Six control sites were included in the analysis (open box).





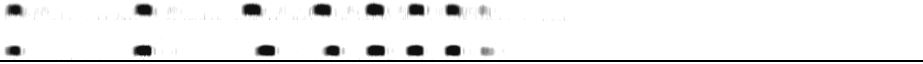


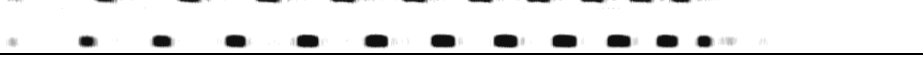


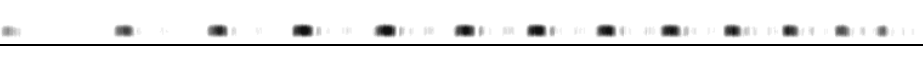


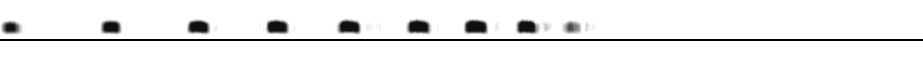


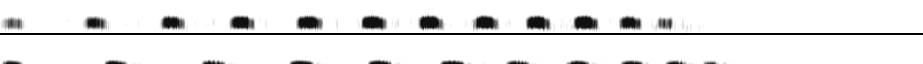
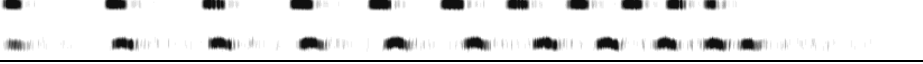


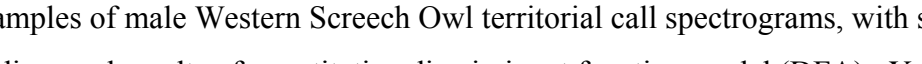
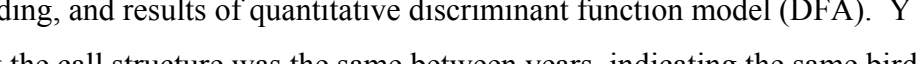
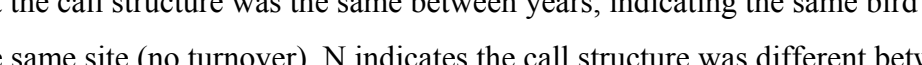
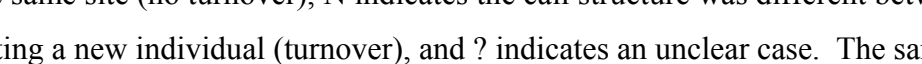
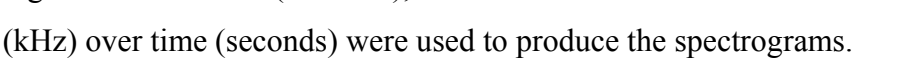

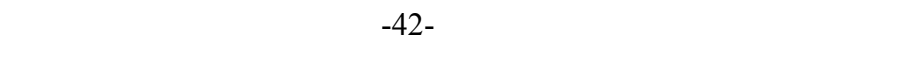

Site	Year	Example of Territorial Call	Result of DFA
1	2002		Y
	2003		
2	2002		?
	2003		
3	2002		Y
	2003		
4	2001		Y
	2002		
5	2002		N
	2003		
7	2002		N
	2003		
8	2002		N
	2003		
9	2001		?
	2003		
17	2002		Y
	2003		
18	2002		?
	2003		
20	2002		?
	2003		
21	2002		?
	2003		
22	2002		N
	2003		
24	2001		Y
	2002		

Fig. 2.3: Examples of male Western Screech Owl territorial call spectrograms, with site and year of recording, and results of quantitative discriminant function model (DFA). Y indicates that the call structure was the same between years, indicating the same bird was present at the same site (no turnover), N indicates the call structure was different between years, indicating a new individual (turnover), and ? indicates an unclear case. The same scale of frequency (kHz) over time (seconds) were used to produce the spectrograms.

2.6 Discussion

I found a high ability to discriminate individual Western Screech-Owls by territorial calls within a breeding season: 87% of test calls were correctly classified against a discriminant function model built using a learning set of calls from the same individuals. My results are thus comparable to several other owl species that have been tested for individual variability (e.g., 80-96% with Wood Owls (Delpont *et al.*, 2002), 84% with Eurasian Pygmy-Owls (Galeotti *et al.*, 1993), and 99% with Tawny Owls (Galeotti and Pavan, 1991). As the calls being classified were not part of the data set used to build the discriminant model, it suggests that the ability to identify male owls throughout a breeding season by call alone is very robust. Discriminant ability was high regardless of whether calls used in classification were taken from a single night or multiple nights across the season, suggesting that call structure does not change appreciably across a single season.

By comparison, the variability of the calls between years may be slightly greater, leading to ambiguity when attempting to monitor male return rates between years based on call structure alone. The performance of the control cases (all at 0% correct classification of calls between years), indicated that I may have set the threshold of $\geq 60\%$ classification between years too high. If the threshold had been reduced to $\geq 50\%$, as per Eakle *et al.* (1989), it would indicate that seven of the 14 sites were occupied by the same bird between years, and the other half were new birds (50% turnover). Based on knowledge of Western Screech-Owl behaviour (non-migratory and territorial year round), high turnover rates were not anticipated. My results were similar to those reported by Galeotti and Sacchi (2001), with an observed 55-78% turnover for Scops Owl (*Otus scops*) territories between two consecutive

breeding seasons. The Scops Owl, however, is likely prone to higher turnover rates due to their migratory nature during the non-breeding season.

In relation to habitat availability, high turnover rates suggest that territories are not a limited resource to the owls. High turnover rates could also reflect a low annual survival of owls, resulting in high rates of turnover where breeding habitat is limited (*i.e.*, unoccupied territories are quickly taken over by new birds). Little is known of annual survival or site turnover rates in screech-owls. Breeding Western Screech-Owls banded at nest boxes in southern Idaho were observed to have an average life span of 1.73 years (range of 1-8, n = 48) for females, and 1.83 (range 1-8, n = 30) for males (cited as pers. comm. In Cannings and Angell, 2001). Similar studies with Eastern Screech-Owls (*Megascops asio*) observed annual survival of 59% in suburban areas and 55% in rural areas (Gehlbach, 1994), and 61-67% annual survival for all adults in northern Idaho (Van Camp and Henny, 1975).

One of the key assumptions in this research was that calls remained stable between years. Research has shown that non-passerines have stable vocalization structure between years, with less variation within than between individuals (Cavanagh and Ritchison, 1987; Galeotti *et al.*, 1993; Appleby and Redpath, 1996; Hill and Lill, 1998; Peake *et al.*, 1998; Delport *et al.*, 2002). The vocalizations of some owls are innate (see review in Delport *et al.* 2002), further suggesting that these vocalizations may remain stable over time. A certain level of variation between years is expected, but overall the differences within birds should be far less than between birds. Environmental effects may cause small differences in recordings between seasons, as noted by Delport *et al.* (2002). High-quality recordings (ideally <25 m from the bird, with low wind conditions and no rain) are therefore essential for between-year

comparison. Only examples of calls in which all notes are clear and sharp should be used for analysis (*i.e.*, to ensure consistent measurements).

My results indicated that the discriminant function analysis technique had a high reliability for identification of individuals within a season, and sufficient ability to assist researchers in long-term monitoring of Western Screech-Owls. Further research, especially cross-validation with individual banding, but also measuring factors that may contribute to vocal variability between years, is required to reach the full potential of vocal individuality as a long-term monitoring tool. The addition of a qualitative spectrogram assessment, especially for ambiguous classifications, may also provide a useful confirmation of quantitative re-identification between years as applied by Galeotti and Sacchi (2001).

A number of papers have indicated the potential use of vocal individuality for long-term monitoring of avian species, but few have actually applied it with this purpose in mind (Eakle *et al.*, 1989; Galeotti *et al.*, 1993; Galeotti and Sacchi, 2001; Peake and McGregor, 2001; Rebbeck *et al.*, 2001; Delport *et al.*, 2002; Gilbert *et al.*, 2002; Terry and McGregor., 2002). Of direct application to species conservation is the understanding of turnover rates within a given population, which could provide information on population trends, and reflect habitat quality and availability. Based on the accuracy of vocal tagging in some species, plus the potential to monitor aspects of individual condition and territory quality through song or call (Godfrey, 2003), the addition of vocal individuality to current inventory and monitoring methods for Western Screech-Owls would be useful for conservation efforts.

3.0 GEOGRAPHIC VARIATION IN THE TERRITORIAL CALL OF MALE WESTERN SCREECH-OWLS IN BRITISH COLUMBIA

3.1 Abstract

Little is known about geographic variation in vocalizations of non-passerines, especially birds of prey. The primary territorial calls of male Western Screech-Owls were examined to determine whether variation was present among populations in British Columbia, Canada. Recordings were collected between February and May 2001-2003 from 46 territories. Seventeen call variables (3 frequency and 14 temporal) were measured from each of 1,354 calls. Three broad regions were sampled representing ranges associated with two recognized subspecies in B.C. (the coastal subspecies *Megascops kennicottii kennicottii*, and the south-central mainland subspecies *M.k. macfarlanei*). In addition, four local populations on the linear southeast-to-northwest cline of the coastal subspecies' (*M.k. kennicottii*) distribution on Vancouver Island were compared. There was a significant difference between vocalizations recorded at the regional scale, with 86.9% correct classification of calls to regions using a modified jackknife test of the forward stepwise discriminant function model. Frequency measurements were the key variables distinguishing between individuals from the three regions. A complete linkage cluster analysis provided additional support for variation at the regional level, indicative of potential dialects. At the sub-regional scale, there appeared to be a gradient in call frequency characteristics from southern to northern Vancouver Island. These results concur with the reproductive isolation of the island vs. mainland interior subspecies, but suggest that the divergence of populations at either extreme of the range on Vancouver Island may be the result of a gradual clinal change.

3.2 Introduction

Among songbirds, geographic variation may occur between populations separated over a broad geographical range, resulting in local song dialects (Catchpole and Slater, 1995). Variation at macro- (regional) and microgeographic (sub-regional) scales has been examined to determine the functional significance of dialects and whether they reflect variation in the behaviour, biology, and habitat use of a species (Galeotti *et al.*, 1996; Latruffe *et al.*, 2000). Much of the research conducted on geographic variation in vocal structure and dialects has focused on its relationship to the Acoustic Adaptation Hypothesis (AAH), which states that song structure may vary between regions due to differential selection on signals imposed by differences in habitat structure (Catchpole and Slater, 1995). Alternate hypotheses that may explain geographic acoustic variation include: 1) reproductive isolation amongst populations (*i.e.*, dialects act as population or group markers to help maintain genetic adaptations to local conditions) (Thielcke, 1973; Naugler and Smith, 1991), 2) life-history traits (*i.e.*, a long life span has been attributed in part to the perpetuation of local dialects) (Avery and Oring, 1977), 3) physiological influences such as size (larger birds produce lower sounds) (Catchpole and Slater, 1995), and 4) overlap avoidance with congeneric species (Doutrelant *et al.*, 1999) (see also Section 1.2). Current research suggests that a combination of factors likely influence regional variation in acoustic structure and function, with no one explanation applying to all species (Date and Lemon, 1993; Ewert and Kroodsma, 1994; Miyasato and Baker, 1999; Baptista, 2000).

The majority of research conducted on geographic variation in song and call structure has focused on passerines (songbirds), as many species have the ability to learn vocalizations, and a tendency towards large, variable song repertoires (Catchpole and Slater, 1995). The

ability of passerines to learn enables them to respond to variations in selective pressure that could result in geographic acoustic variation (Catchpole and Slater, 1995). In contrast, few studies have examined geographic variation in vocalizations of non-songbirds, especially birds of prey, which are usually neglected in questions of acoustic geographical variability because their vocalizations are regarded as invariant (Martens, 1996). This is in part due to the widely held belief that, as the calls of non-songbirds are innate and often simple in structure, they are less plastic to respond to slight variations in selective pressure that differentially influence disjunct populations (Catchpole and Slater, 1995; König *et al.*, 1999). This often results in less focus on these species by researchers interested in the adaptive significance of dialects. Yet if calls are innate, slight variation in call structure may reflect reproductively isolated populations in non-passerines. In fact, call variation is often used to distinguish taxonomy at the species and subspecies levels for highly-vocal, non-passerines, such as the genera *Glaucidium* and *Megascops* (the latter formerly *Otus*, recently split into *Otus* and *Megascops*; American Ornithologists' Union, 2003) (Johnsgard, 1988; König *et al.*, 1999). As such, dialectal variation among disparate populations may give insight into the taxonomic relationships between groups where current subspecific designations are questionable.

Recent studies of the Tawny Owl (*Strix aluco*) (Appleby and Redpath, 1996; Galeotti *et al.*, 1996) suggest that regional and local dialects exist in this species. Hoot variation in Tawny Owls, suggests that vocally distinct populations may be reproductively isolated. Similar studies have also found dialectal variation among disparate populations in the White-faced Scops Owl (*Ptilopsis sagittatus*) (Weydenvander, 1973) and the Little Owl (*Athene noctua*)

(Exo, 1990), suggesting further that differences in vocal structure may reflect reduced gene flow between these populations.

I was interested in determining whether similar dialectal variation occurred within Western Screech-Owls in Canada, where at least two distinct, geographically isolated subspecies are presently recognized. In addition, at one time a third subspecies from B.C., *M. k. saturatus*, was described by Brewster in 1891 as paler and smaller than *M. k. kennicottii*, and restricted to southeastern Vancouver Island and the Gulf and San Juan Islands (Hekstra 1982) (Section 1.4). I was interested, therefore, in also comparing call structure among local populations from southeastern and northern Vancouver Island to determine whether variation was present in support of the *M. k. saturatus* subspecies designation.

The Western Screech-Owl is a nocturnal, secretive, highly vocal, long-lived, non-migratory species that is fairly common throughout most of its range in western North America (Cannings and Angell, 2001). It is found in a wide variety of habitats including deciduous hardwood, coniferous, and mixed stands, and could therefore be subject to the acoustic constraints of a variety of vegetated environments.

All owls of the genus *Otus/Megascops* are separated taxonomically to some degree by call (Konig *et al.*, 1999). Presently nine subspecies of *Megascops kennicottii* are recognized in North America (Gehlbach, 2003). Up to 18 subspecies of Western Screech-Owl were previously recognized, based primarily on vocal and morphological descriptions from a small number of specimens (Hekstra, 1982; Johnsgard, 1988). It is now suspected that some of the variation in calls used to classify the 18 subspecies may have been a result of individual variation among the birds sampled (Konig *et al.*, 1999). In a recent species account,

Cannings and Angell (2001) suggested the need to study geographic variation in the vocalizations of this species, as the current subspecific designations may not represent the true meta-structure of the species. Undertaking such studies, however, requires that calls from numerous individuals within microgeographic regions be sampled to account for individual variation in call structure versus variation that occurs among populations (Galeotti and Pavan, 1991; Galeotti *et al.*, 1993; Appleby and Redpath, 1996).

The primary objectives of this study were: 1) to determine whether regional variation was present between the primary territorial call structure of two currently recognized subspecies, 2) to determine whether variation in call structure was present at the sub-regional scale among local populations recorded from Vancouver Island, and 3) to examine whether call variation among individuals (vocal individuality) functioned at a high level of classification within a given population (examined separately for each region and sub-region), and at the same time allowed correct classification of individuals to their region of origin (*i.e.*, was there high individual, as well as regional, variation?).

3.3 Methods

3.3.1 Study Area

To achieve my objectives I recorded the calls of multiple resident male owls during the breeding season (February to May, 2001 to 2003) from southern (Victoria and Duncan), central (Campbell River), and northern (Nimpkish Valley) (southern and northern populations) on Vancouver Island representing the *M. k. kennicottii* subspecies. In addition, I recorded calls from Western Screech-Owls in south-central B.C. (Okanagan Valley), representing the *M.k. macfarlanei* subspecies (Gehlbach, 2003) (Fig. 1.1). An overview description of habitats within each of the study areas is provided in Chapter 1 (Section 1.6).

3.3.2 *Field Methods and Spectrographic Analysis*

The same methods for data collection and spectrographic analysis were applied to this study as outlined previously in Chapter 2 (Section 2.3.2). Recordings were collected between February and May 2001-2003 from 46 territories (Appendix 1). The same 17 variables (3 frequency and 14 temporal) were measured from each of 1,354 territorial calls (Fig. 2.1). For the purpose of establishing macro- and microgeographic regions, distances between owl territories were measured in kilometres using ArcView 3.2 geographical information software (ESRI Canada, Toronto, Ontario) (ESRI, 2000). For my study I defined macrogeographic populations (regions) as being separated by >250 km, while distances between microgeographic (sub-region or local) populations examined on Vancouver Island were >30 km (31 km between Victoria and Duncan, 170 km between Duncan and Campbell River, and 60 km between Campbell River and the Nimpkish Valley) (Fig. 1.1). Based on information available on average natal dispersal distances for this species (an average of 14.7 km based on data from 13 females, and 5.1 km based on data from 15 males from southern Idaho research; Ellsworth and Belthoff, 1997), the >30 km designation to separate sub-regions may reflect a reduced potential for gene exchange between populations.

3.4 Analysis

3.4.1 *ANOVA and Cluster Analyses*

Because multiple calls were recorded from each male within each region and sub-region, an average value for all territorial call measures for each individual was calculated to use in dialectal analyses across populations. These averages were based on a mean of 30 recorded calls per territory. A single, averaged value for each bird was used to compare calls between regions to avoid problems associated with pseudoreplication.

A series of one-way ANOVA were used to test for significant differences amongst call variables between populations. A sequential Bonferroni correction for multiple tests (Rice, 1989) was applied to p-values to ensure a more conservative test. A Scheffe's post-hoc test was then conducted on frequency variables that remained significant following the Bonferroni correction. Variables indicated as significantly different in the corrected one-way ANOVAs were entered into a complete linkage, Euclidean distance cluster analysis to examine potential groupings of individuals into macro- and microgeographic populations.

Data were standardized to ensure equal weight in the cluster analyses, for results entirely independent of the ranges of values or the units of measurement (Zar, 1984). The number of groups indicated by the cluster analysis was identified based on interpretation of the plateau from the graphed amalgamation schedule. The plateau indicated that clusters were formed at essentially the same linkage distance, which was considered to be the optimal distance for the number of clusters to interpret (StatSoft, 2002).

3.4.2 Discriminant Function Analyses

To investigate regional and sub-regional variation further, discriminant function analyses (DFA) (p to enter = 0.05) were conducted using Statistica 6.0 (StatSoft, 2002). Data were not standardized prior to this analysis because the outcome of a DFA is not affected by the scaling of individual variables (Manly, 1994; Quinn and Keough, 2002). All 17 territorial call variables were assessed for their ability to correctly classify individuals to their population of origin.

To determine whether variation in call structure existed between regions, a total of 32 individuals, representing three regions separated by >250 km, were included in the analysis

(13 from Victoria on southern Vancouver Island, 9 from the Nimpkish Valley on northern Vancouver Island, and 10 from south-central B.C.). At the sub-regional scale, 36 individuals were included in the DFA (13 from Victoria, 9 from Duncan, 5 from Campbell River, and 9 from Nimpkish Valley).

Due to the small sample size of individuals representing each geographic population, a modified jackknife procedure was applied as a cross-validation of the DFA models. One individual from each region was excluded from the remaining individuals, the latter of which was used to create the discriminant model. The model was then tested by attempting to classify the excluded individuals into their macrogeographic region of origin. This procedure was run nine times, with three different individuals excluded in each run, to develop a conservative estimate of the discriminant ability of the model to classify novel individuals into their macrogeographic region of origin. A similar modified jackknife analysis was conducted when assigning males on the southeast/northwest cline of Vancouver Island to sub-regional populations using DFA.

In addition, a series of DFA's were run to assess discriminant performance within each region for vocal individuality (southern Vancouver Island: 388 calls from 13 owls, northern Vancouver Island: 254 calls from 9 owls, and the south-central mainland: 293 calls from 10 owls). The larger sample size available for vocal individuality (calls as opposed to individuals) allowed the use of two datasets, one set of calls to build the model and another set for cross-validation. Unlike previous vocal individuality research on Western Screech-Owls (Chapter 2), this analysis focused on individual variation within each of the three regions and four sub-regions examined for variation in call structure. This analysis was

included to determine whether call structure was variable enough to allow for high correct classification of individuals to the regions and sub-region where recordings were collected. I examined classification of territorial calls to individuals (vocal individuality) within each population, and compared the results to the regional and sub-regional DFA performances.

3.5 Results

Subsequent to the more conservative test with Bonferroni correction, only the three frequency variables (F1, F2, and F3) remained significantly different (p-value <0.05) between the three regions (Table 3.1). The south-central mainland (Region 3) appeared to be most easily distinguished from the other two regions by lower call frequency values (F1-F3), with frequency at start of call averaging 593 Hz compared to 672 Hz for southern Vancouver Island, and 627 Hz for northern Vancouver Island (Region 1 and Region 2, respectively) (Table 3.1).

Table 3.1: Male Western Screech-Owl mean territorial call measures and associated one-way ANOVA's amongst three regions (Region 1 (southern Vancouver Island), Region 2 (northern Vancouver Island), and Region 3 (south-central mainland of B.C.)) ($n = 32$ owls in total). Variables that were significant between regions after sequential Bonferroni correction of p-values < 0.05 are indicated in bold.

Variables	Var. ID	Region 1		Region 2		Region 3		One-way ANOVA Amongst Regions	
		Mean ($n=13$)	S.D.	Mean ($n=9$)	S.D.	Mean ($n=10$)	S.D.	F value (2, 29)	p-value
#Notes/Call	R1	11.313	2.726	11.678	1.471	11.354	1.781	0.084	0.918
Ratio Internote 2/5	R2	1.787	0.284	1.860	0.276	1.742	0.107	0.578	0.567
#Notes/Second	R3	6.403	0.904	6.513	0.631	6.484	0.581	0.066	0.936
Total Length of Call (sec)	D1	1.755	0.244	1.799	0.189	1.755	0.246	0.114	0.893
Internote 1 (sec)	D2	0.246	0.041	0.225	0.019	0.218	0.027	2.465	0.103
Internote 2 (sec)	D3	0.219	0.030	0.212	0.017	0.209	0.020	0.507	0.608
Internote 3 (sec)	D4	0.202	0.025	0.200	0.013	0.197	0.017	0.148	0.863
Internote 4 (sec)	D5	0.140	0.028	0.135	0.021	0.138	0.018	0.145	0.865
Internote 5 (sec)	D6	0.125	0.022	0.117	0.022	0.121	0.015	0.396	0.676
Internote 6 (sec)	D7	0.109	0.016	0.105	0.018	0.105	0.012	0.291	0.749
Mean Freq. at Start (Hz)	F1	672.94	21.53	627.72	27.77	593.47	32.50	24.86	<0.001
Mean Freq. at End (Hz)	F2	675.69	53.98	645.30	36.25	603.56	36.44	14.52	<0.001
Freq. at Peak Amp. (Hz)	F3	697.66	20.57	678.55	46.79	634.99	41.62	8.59	<0.001
Note Length 1 (sec)	N1	0.055	0.005	0.051	0.002	0.054	0.004	2.834	0.075
Note Length 2 (sec)	N2	0.057	0.004	0.053	0.002	0.059	0.004	5.606	0.008
Note Length 3 (sec)	N3	0.055	0.006	0.051	0.005	0.058	0.004	4.487	0.020
Note Length 4 (sec)	N4	0.051	0.005	0.048	0.004	0.054	0.004	3.233	0.054

The Scheffe's post-hoc test, conducted on the three frequency variables that remained significant following the Bonferroni correction, indicated that the mean frequency of the second note (F1) was significantly different among all three regions. The F1 measure varied the most between calls recorded on southern Vancouver Island and the south-central mainland, and least between northern Vancouver Island and the south-central mainland, with F1 variability intermediate between southern and northern Vancouver Island (Table 3.2).

Table 3.2: Summary of Scheffe’s post-hoc tests following Bonferroni-corrected ANOVAs for significant call frequency variables of Western Screech-Owls ($n = 32$) among three regions (Region 1 (southern Vancouver Island), Region 2 (northern Vancouver Island), and Region 3 (south-central mainland)). Significant results are indicated in bold ($p < 0.05$, $df = 29$).

Variables Compared in Scheffe’s post-hoc test			
Regions Compared	F1 (Mean frequency at start of call) p-values	F2 (Mean frequency at end of call) p-values	F3 (Frequency at peak amplitude of call) p-values
1 and 2	0.0025	0.1062	0.4871
2 and 3	0.0344	0.0276	0.0466
1 and 3	0.0000	0.0000	0.0013

In contrast, mean frequency at the end of a call (F2), showed no significant difference between southern and northern Vancouver Island. The greatest variability for measure F2 was between southern Vancouver Island and south-central mainland, with intermediate results between northern Vancouver Island and the south-central mainland. Similar results were indicated in the post-hoc test for the third frequency measure, frequency at peak amplitude (F3), with no significant difference between southern and northern Vancouver Island, and the greatest variation between southern Vancouver Island and the south-central mainland of B.C. (Table 3.2).

Results of the univariate analysis at the sub-regional scale indicated that call structure did not vary significantly between the four populations on Vancouver Island (Table 3.3). As no variables remained significantly different after the sequential Bonferroni correction was applied, no post-hoc test or cluster analysis was included.

Table 3.3: Male Western Screech-Owl mean territorial call characteristics and associated one-way ANOVA's amongst four sub-regions along a southeast/northwest cline of Vancouver Island (A (Victoria), B (Duncan), C (Campbell River), and D (Nimkish Valley)) ($n = 36$ owls in total). P-value was set at <0.05 in the one-way ANOVAs. No variables remained significant after Bonferroni correction.

Variables	Var. ID	Sub-Region A		Sub-Region B		Sub-Region C		Sub-Region D		One-way ANOVAs	
		Mean ($n = 13$)	S.D.	Mean ($n = 9$)	S.D.	Mean ($n = 5$)	S.D.	Mean ($n = 9$)	S.D.	F value (3,32)	p-value
#Notes/Call	R1	11.313	2.726	10.237	1.845	11.500	1.708	11.678	1.471	0.805	0.5002
Ratio Internote 2/5	R2	1.787	0.284	1.836	0.475	1.757	0.244	1.860	0.276	0.145	0.9320
#Notes/Second	R3	6.403	0.904	5.871	0.509	6.563	0.224	6.513	0.631	1.771	0.1724
Total Length of Call (sec)	D1	1.755	0.244	1.742	0.254	1.756	0.282	1.799	0.189	0.096	0.9615
Internote 1 (sec)	D2	0.246	0.041	0.268	0.041	0.220	0.020	0.225	0.019	3.172	0.0374
Internote 2 (sec)	D3	0.219	0.030	0.237	0.027	0.206	0.011	0.212	0.017	2.339	0.0920
Internote 3 (sec)	D4	0.202	0.025	0.210	0.016	0.194	0.008	0.200	0.013	0.802	0.5016
Internote 4 (sec)	D5	0.140	0.028	0.152	0.029	0.134	0.011	0.135	0.021	0.926	0.4389
Internote 5 (sec)	D6	0.125	0.022	0.135	0.027	0.119	0.013	0.117	0.022	1.059	0.3801
Internote 6 (sec)	D7	0.109	0.016	0.120	0.024	0.106	0.013	0.105	0.018	1.134	0.3500
Mean Freq. at Start (Hz)	F1	672.94	21.53	663.28	24.42	645.56	48.16	627.72	27.77	4.936	0.0062
Mean Freq. at End (Hz)	F2	675.69	53.98	674.31	20.64	653.50	46.62	645.30	36.25	2.318	0.0941
Freq. at Peak Amp. (Hz)	F3	697.66	20.57	690.05	24.35	677.22	54.79	678.55	46.79	0.714	0.5507
Note Length 1 (sec)	N1	0.055	0.005	0.051	0.005	0.052	0.003	0.051	0.002	2.372	0.0887
Note Length 2 (sec)	N2	0.057	0.004	0.053	0.005	0.055	0.002	0.053	0.002	2.324	0.0934
Note Length 3 (sec)	N3	0.055	0.006	0.053	0.007	0.053	0.004	0.051	0.005	0.875	0.4640
Note Length 4 (sec)	N4	0.051	0.005	0.051	0.006	0.050	0.003	0.048	0.004	0.584	0.6297

3.5.1 Cluster Analyses

The cluster analysis, based on the three frequency variables that were significantly different between regions in the analysis above, indicated three distinct clusters, which diverge at linkage distance four (Fig. 3.1).

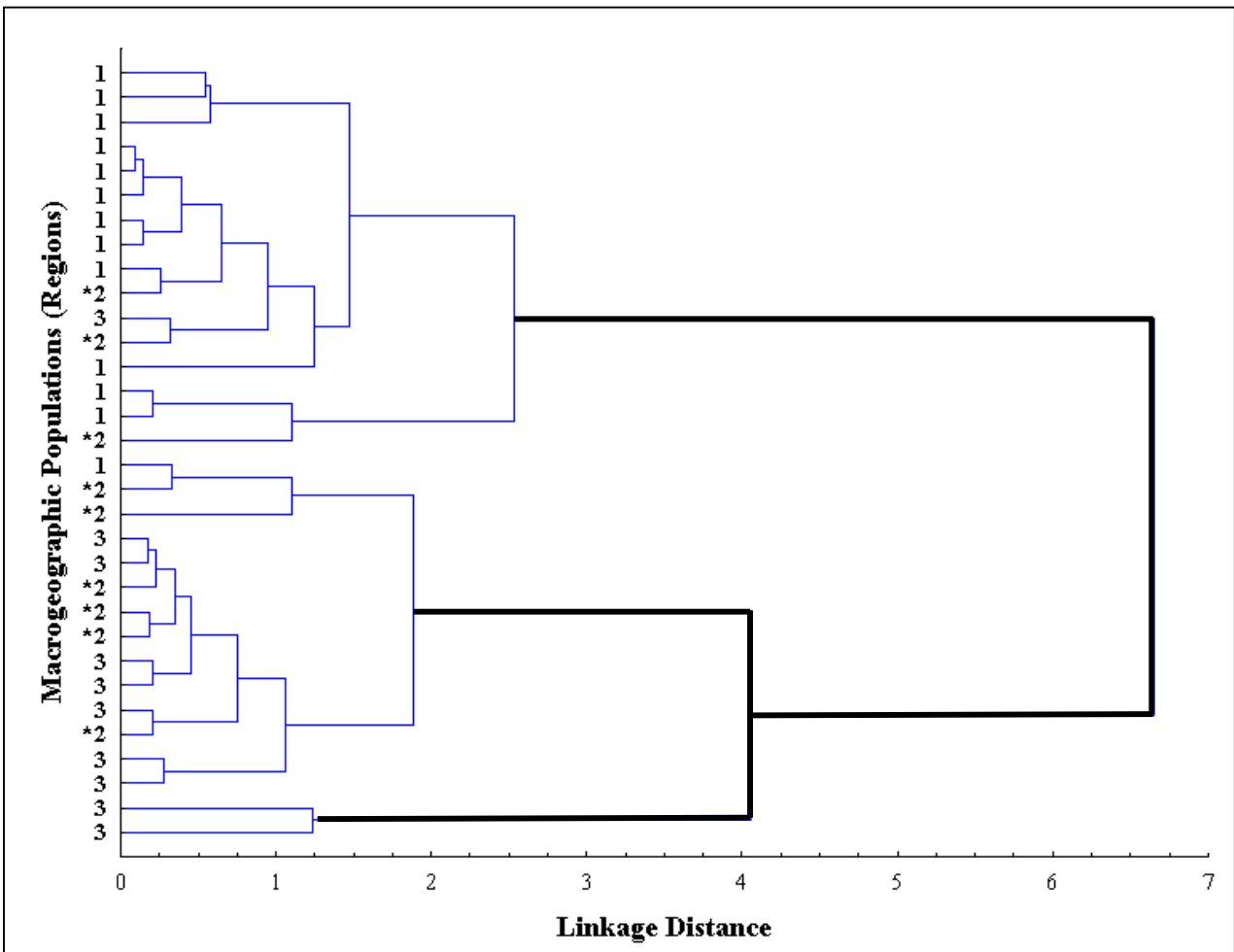


Fig. 3.1: Complete linkage, Euclidean distance cluster analysis of male Western Screech-Owl territorial calls from Regions 1 (southern Vancouver Island), *2 (northern Vancouver Island), and 3 (south-central B.C.) based on three variables (F1, F2, and F3). * indicate birds from Region 2 that may represent an intermediate call structure from Regions 1 and 3.

These three groupings indicated that southern Vancouver Island birds were most distinct, while birds from the other two regions (south-central mainland and northern Vancouver Island) tended to be more intermingled in clustering. Specifically, birds from northern Vancouver Island appeared more difficult to group, and were widely spread amongst two of the three clusters (denoted by asterisks in Fig. 3.1). The intermediate classification of calls from northern Vancouver Island were similar to the findings from the post-hoc test (Table 3.2).

3.5.2 Discriminant Function Analyses

Across the three macrogeographic populations, an average of 90.6% of the individuals could be correctly classified to their region of origin (Table 3.4). As a conservative estimate of discriminant ability, a modified jackknife resulted in an average of 86.9% correct classification. Region 1 (southern Vancouver Island) birds were not misclassified, while Region 2 (northern Vancouver Island) birds were misclassified twice to Region 1, and twice to Region 3 (south-central B.C.). Of the ten birds representing Region 3, one was misclassified as Region 2 (Table 3.4).

Table 3.4: Summary of discriminant function analysis (DFA) and modified jackknife test between territorial call structure of male Western Screech-Owls from three regions (1 = southern Vancouver Island, 2 = northern Vancouver Island, and 3 = south-central mainland) ($n = 32$, F-to-enter 1.0, $p = 0.05$, 17 variables entered, $df = 2$).

Region	No. of birds	Region	% Correct Classification (DFA model)	Classification of All Individuals			
				Region 1	Region 2	Region 3	
1 (s. Van. Island)	13	1	100.0%	13	0	0	
2 (n. Van. Island)	9	2	77.8%	2	7	0	
3 (south-central B.C.)	10	3	90.0%	0	1	9	
Totals	32		$\bar{x} = 90.6\%$	15	8	9	
			% Correct Classification (DFA minus Jackknife cases)	Jackknife Class.	Classification of Individuals in Jackknife		
		1	83.33-100 ($\bar{x} = 94.4\%$)	100%	9	0	0
		2	37.50-87.50 ($\bar{x} = 75.0\%$)	55.6%	2	5	2
		3	88.88-100 ($\bar{x} = 91.3\%$)	88.9%	0	1	8
Totals			Overall $\bar{x} = 86.9\%$		11	6	10

Variables that contributed the most to the multivariate discriminant models varied slightly from those indicated by univariate analyses. Five variables that were indicated as having sufficient variability between regions (high F values) to enter into the DFA model included F1, F3, N1, N2, and N3 (Table 3.5). Because the modified jackknife DFA was run nine times, each with a different combination of individuals, the variables with the highest discriminant ability varied slightly between models. All nine of the modified jackknife tests indicated that the average frequency at the start of the call (F1) had the greatest discriminant ability amongst regions, while the frequency at peak amplitude (F3) was only significant in the final step of the model for four of the nine jackknife tests. Lengths of the second and third notes (N1 and N2) were included in the final step of the discriminant model in seven of the nine jackknife tests, while note length of the third from last note (N3) was only included in one.

Table 3.5: F values of variables included in the discriminant function analysis for classification of male Western Screech-Owl territorial calls from Regions 1, 2 and 3 ($n = 32$, F-to-enter 1.0, $p = 0.05$, 17 variables entered, $df = 2$). The F-to-enter and p-value columns represent the resultant model when all individuals were entered in the DFA. Significant results are indicated in bold.

Variable	F-to-enter 1.0	p-value	Variables entered in Jackknife DFA Models
R1 (# notes/call)	0.554	0.580	
R2 (Ratio of 2 nd Internote to 4 th Internote Measure)	0.013	0.986	
R3 (#notes/second)	1.482	0.245	
D1 (Total Length of Call)	0.238	0.789	
D2 (Internote distance between note #1 and #2)	0.048	0.952	
D3 (Internote distance between note #2 and #3)	0.525	0.597	
D4 (Internote distance between note #3 and #4)	1.064	0.359	
D5 (Internote distance between fourth from last note and third from last note)	1.090	0.350	
D6 (Internote distance between third from last note and second from last note)	0.223	0.801	
D7 (Internote distance between last two notes)	0.158	0.854	
F1 (Mean frequency at start of call, note #2)	16.710	<0.001	9 of 9 jackknife tests F range (8.059-23.332) p-value (0.002-0.000)
F2 (Mean frequency at end of call)	1.869	0.174	
F3 (Frequency at peak amplitude)	3.147	0.059	4 of 9 jackknife tests F range (3.546-4.526) p-value (0.045-0.020)
N1 (Length of second note)	10.637	<0.001	7 of 9 jackknife tests F range (7.298-22.943) p-value (0.003-0.000)
N2 (Note length of third note)	15.060	<0.001	7 of 9 jackknife tests F range (10.816-29.013) p-value (0.000-0.000)
N3 (Note length of third from last note)	0.004	0.995	1 of 9 jackknife tests F value (4.402) p-value (0.023)
N4 (Note length of second from last note)	0.008	0.991	

At the sub-regional scale, the DFA did not perform well in correctly classifying birds to their population of origin on Vancouver Island. The modified jackknife analysis resulted in a 48.1% average in the model, and 30.6% for the jackknife classifications, with Victoria and Nimpkish Valley birds most consistently classified correctly (Table 3.6).

Table 3.6: Summary of discriminant function analysis and modified jackknife test for classification of male territorial calls of Western Screech-Owls occupying local populations (sub-regions) along a southeast/northwest cline of Vancouver Island ($n = 36$, F-to-enter 1.0, $p = 0.05$, 17 variables entered, $df = 3$).

Sub-Region	# of birds	% Correct Classification (DFA model)	Classification per Sub-Region (All Individuals)				
			A	B	C	D	
A (Victoria)	13	84.6%	A	11	0	0	2
B (Duncan)	9	0.0%	B	7	0	0	2
C (Campbell River)	5	20.0%	C	2	0	1	2
D (Nimpkish Valley)	9	88.9%	D	1	0	0	8
Totals	36	$\bar{x} = 55.6\%$		21	0	1	14

% Correct Classification (DFA model minus test cases for Jackknife)	Jackknife Class.	Classification of Individuals in Jackknife				
		A	B	C	D	
75-91 ($\bar{x} = 85.2\%$)	77.8%	A	7	1	1	0
0-75% ($\bar{x} = 15.3\%$)	0.0%	B	6	0	1	2
0-60% ($\bar{x} = 18.3\%$)	0.0%	C	2	0	0	3
0-87.5% ($\bar{x} = 73.6\%$)	44.4%	D	3	1	1	4
Totals	Overall $\bar{x} = 48.1\%$	30.6%	18	2	3	9

Only two variables provided discriminant ability in the DFA model, F1 ($F = 8.49$), and F3 ($F = 3.40$). As a result of different combinations of individuals used in the modified jackknife analyses, three additional variables showed discriminant ability (note length measure one and two (N1, N2), and internote distance between the first and second note of the call (D2)) (Table 3.7).

Table 3.7: F values of variables included in the discriminant function analysis and the modified jackknife DFA for microgeographic classification of male Western Screech-Owls territorial calls on Vancouver Island, British Columbia ($n = 36$, F-to-enter 1.0, $p = 0.05$, 17 variables entered, $df = 3$). The F-to-enter and p-value columns represent the resultant model when all individuals were entered in the DFA. Significant results are indicated in bold.

Variable	F-to-enter 1.0	p-value	Variables entered in Jackknife DFA Models
R1 (# notes/call)	0.558	0.646	
R2 (Ratio of 2 nd Internote to 4 th Internote Measure)	0.168	0.916	
R3 (#notes/second)	1.381	0.267	
D1 (Total length of call)	0.007	0.999	
D2 (Internote distance between note #1 and #2)	1.776	0.172	2 of 9 jackknife tests F range (4.437-9.706) p-value (0.011-0.000)
D3 (Internote distance between note #2 and #3)	1.769	0.174	
D4 (Internote distance between note #3 and #4)	0.654	0.586	
D5 (Internote distance between fourth from last note and third from last note)	0.643	0.592	
D6 (Internote distance between third from last note and second from last note)	0.630	0.600	
D7 (Internote distance between last two notes)	0.805	0.500	
F1 (Mean frequency at start of call, note #2)	8.496	<0.001	8 of 9 jackknife tests F range (5.147-8.298) p-value (0.005-0.000)
F2 (Mean frequency at end of call)	1.093	0.367	
F3 (Frequency at peak amplitude)	3.400	0.029	5 of 9 jackknife tests F range (2.972-4.009) p-value (0.049-0.017)
N1 (Length of second note)	1.712	0.185	2 of 9 jackknife tests F range (3.583-10.498) p-value (0.026-0.000)
N2 (Note length of third note)	1.451	0.247	1 of 9 jackknife tests F value (3.673) p-value (0.024)
N3 (Note length of third from last note)	0.668	0.578	
N4 (Note length of second from last note)	0.194	0.899	

In addition, a discriminant function analysis was performed to determine the level of vocal individuality within each of the three regions and four sub-regions. This DFA resulted in a 91.4% correct call classification within southern Vancouver Island, 98.8% within northern Vancouver Island, and 96.8% within the south south-central B.C. (Table 3.8).

Table 3.8: F-values of variables included in the discriminant function model for classification of male Western Screech-Owl territorial calls within three regions (1 (southern Vancouver Island), 2 (northern Vancouver Island), and 3 (south-central B.C.)) ($n = 32$ sites in total, F-to-enter 5.0, $p = 0.05$, 17 variables entered, degrees of freedom = 27). The top four variables from each model have been bolded to indicate measured call characteristics that showed the greatest discriminant ability between individuals within the DFA model for each macrogeographic region.

Regional Study Areas							
Variables	Var. ID	Region 1 ($n=13$)		Region 2 ($n=9$)		Region 3 ($n=10$)	
		F-value	p-value	F-value	p-value	F-value	p-value
Number of Notes/Call	R1	48.60	<0.001	15.88	<0.001	20.48	<0.001
Ratio Internote D2/D5	R2	19.84	<0.001	39.12	<0.001	5.19	<0.001
Number of Notes/Second	R3	21.02	<0.001	0.99	0.445	18.76	<0.001
Total Length of Call (sec)	D1	44.64	<0.001	11.47	<0.001	28.74	<0.001
Internote 1 (sec)	D2	16.95	<0.001	10.69	<0.001	32.39	<0.001
Internote 2 (sec)	D3	18.77	<0.001	10.35	<0.001	7.09	<0.001
Internote 3 (sec)	D4	6.27	<0.001	3.76	<0.001	3.49	<0.001
Internote 4 (sec)	D5	4.32	<0.001	3.06	0.003	5.48	<0.001
Internote 5 (sec)	D6	12.64	<0.001	4.39	<0.001	6.25	<0.001
Internote 6 (sec)	D7	4.41	<0.001	13.72	<0.001	3.35	<0.001
Mean Freq. at Start (Hz)	F1	14.20	<0.001	8.80	<0.001	14.38	<0.001
Mean Freq. at End (Hz)	F2	4.77	<0.001	6.55	<0.001	4.58	<0.001
Freq. at Peak Amp. (Hz)	F3	12.76	<0.001	60.02	<0.001	31.85	<0.001
Note Length 1 (sec)	N1	14.64	<0.001	3.84	<0.001	4.39	<0.001
Note Length 2 (sec)	N2	1.65	0.078	3.36	0.001	2.83	0.004
Note Length 3 (sec)	N3	3.06	<0.001	2.60	0.010	2.06	0.035
Note Length 4 (sec)	N4	1.68	0.072	4.76	<0.001	3.34	<0.001
Correct Individual Call Classification of Model		96.2%		94.8%		98.0%	
Correct Individual Call Classification of Cross-Validation		91.4%		98.8%		96.8%	

Variables that accounted for the greatest variation between individuals within each region were different amongst the three DFA models. Variables that showed the highest discriminant ability within each of the regions were number of notes per call (R1, $F = 46.63$) for southern Vancouver Island, frequency at peak amplitude (F3, $F = 60.01$) for northern Vancouver Island, and internote distance between first and second note (D2, $F = 32.39$) for the south-central mainland population (Table 3.8).

The four DFA models, conducted at the sub-regional scale for vocal individuality, resulted in 91.4% correct call classification in the cross-validation for Victoria, 86.5% for Duncan, 91.8% for Campbell River, and 98.8% for the Nimpkish Valley (Table 3.9). Variables that accounted for the greatest variation between individuals within each sub-region were similar to those at the regional scale, in part because the same birds from Victoria and the Nimpkish Valley were used in comparisons conducted at both scales. Variable R2 (ratio of internote measurement $D3/D6$), which represents how quickly the call speeds up towards the end, demonstrated high discriminant ability within all four of the sub-regional DFA models (Table 3.9).

Table 3.9: F values of variables included in the discriminant function model for classification of male Western Screech-Owl territorial calls within four sub-regions: A (Victoria), B (Duncan), C (Campbell River), and D (Nimpkish Valley) ($n = 36$ sites in total, F-to-enter 5.0, $p = 0.05$, 17 variables entered, degrees of freedom = 27). The top four variables from each model have been bolded to indicate measured call characteristics that showed the greatest discriminant ability between individuals within the DFA model for each sub-region.

Sub-Regional Study Areas on Vancouver Island									
Variables		Victoria ($n=13$)		Duncan ($n=9$)		Campbell River ($n=5$)		Nimpkish Valley ($n=10$)	
		F-value	p-value	F-value	p-value	F-value	p-value	F-value	p-value
Number of Notes/Call	R1	48.600	<0.001	14.787	<0.001	16.140	<0.001	15.880	<0.001
Ratio Internote D2/D5	R2	19.841	<0.001	15.524	<0.001	24.177	<0.001	39.120	<0.001
Number of Notes/Second	R3	21.021	<0.001	9.774	<0.001	14.906	<0.001	0.990	0.445
Total Length of Call (sec)	D1	44.642	<0.001	14.910	<0.001	2.275	0.067	11.469	<0.001
Internote 1 (sec)	D2	16.947	<0.001	32.732	<0.001	33.465	<0.001	10.685	<0.001
Internote 2 (sec)	D3	18.766	<0.001	8.431	<0.001	3.096	0.019	10.345	<0.001
Internote 3 (sec)	D4	6.269	<0.001	15.153	<0.001	0.379	0.822	3.757	<0.001
Internote 4 (sec)	D5	4.317	<0.001	7.992	<0.001	0.399	0.808	3.064	0.003
Internote 5 (sec)	D6	12.640	<0.001	10.297	<0.001	0.760	0.553	4.393	<0.001
Internote 6 (sec)	D7	4.412	<0.001	5.367	<0.001	5.235	<0.001	13.716	<0.001
Mean Freq. at Start (Hz)	F1	14.195	<0.001	7.978	<0.001	6.873	<0.001	8.801	<0.001
Mean Freq. at End (Hz)	F2	4.767	<0.001	1.644	0.116	1.817	0.132	6.550	<0.001
Freq. at Peak Amp. (Hz)	F3	12.757	<0.001	9.733	<0.001	15.879	<0.001	60.016	<0.001
Note Length 1 (sec)	N1	14.644	<0.001	2.768	0.006	20.492	<0.001	3.836	<0.001
Note Length 2 (sec)	N2	1.652	0.078	7.479	<0.001	1.028	0.397	3.363	<0.001
Note Length 3 (sec)	N3	3.056	<0.001	6.309	<0.001	1.609	0.178	2.600	0.010
Note Length 4 (sec)	N4	1.678	0.072	2.891	0.004	2.794	0.030	4.759	<0.001
Correct Individual Call Classification of Model		96.2%		96.7%		99.0%		94.8%	
Correct Individual Call Classification of Cross-Validation		91.4%		86.5%		91.8%		98.8%	

3.6 Discussion

All analyses indicated differences in call structure amongst the three regions, supportive of dialects and possible reproductive isolation. The Scheffe's post-hoc test and cluster analysis indicated that the northern Vancouver Island call structure was intermediate to that of southern Vancouver Island and the south-central mainland of B.C. At the sub-regional scale, call characteristics did not appear to be distinct between local populations. Rather, a gradual change in frequency variables was apparent along the latitudinal cline of owl populations on Vancouver Island, with the lowest frequencies in the north and the highest in the south. A similar pattern was observed from east to west, with lowest call frequency characteristics in the south-central mainland subspecies *M.k. macfarlanei* (east) compared to the Vancouver Island subspecies *M.k. kennicottii* (west). Vocal individuality remained highly distinct within each of the three regions.

There are a number of hypotheses that attempt to explain why geographic variation in vocal structure occurs in avian species, one of which is the Acoustic Adaptation Hypothesis (AAH). It indicates that birds occupying open habitat should have vocalizations of higher frequency than birds inhabiting dense vegetation, due to reverberation and acoustic degradation resulting from travelling through dense vegetation (*i.e.*, sound travels better at lower frequencies through dense habitat) (Catchpole and Slater, 1995). My results were contrary to what would be expected based on the AAH, with the south-central mainland subspecies having lower frequency characteristics even though they were associated with more open habitat than coastal birds (open deciduous, riparian forest, versus dense predominately coniferous forest on the coast). The fact that the two regions with the lower call frequencies (northern Vancouver Island and south-central mainland) occupied such

different habitat conditions indicated that the AAH may not provide a viable explanation for the observed regional differences.

Although variation in frequency (pitch) between populations occupying contrasting habitat types (open versus closed) did not appear to be explained by the AAH, call structure of the Western Screech-Owl may lend support to the theory in other aspects. For example, the primary territorial call consists of low frequency, well-spaced notes ideally suited for long-range transmission through forested habitat. The gaps between notes likely minimize reverberations in dense vegetation (Wiley and Richards, 1982). As trills, consisting of more tightly spaced notes, transmit poorly through dense vegetation (Doutrelant *et al.*, 1999), it might explain why Western Screech-Owls use the ‘bounce’ call for long-distance territorial communication.

One of the simplest explanations of the observed regional variation in adult male Western Screech-Owls could be a result of body size, with lower frequencies attributed to bigger birds (Johnsgard, 1988). Birds from the south-central mainland of B.C., representing the *M.k. macfarlanei* subspecies, are known to be the largest of the eight subspecies recognized in North America (Cannings and Angell, 2001). The observed trend in size for this species in North America is of largest birds in the north and smallest in the south (Gehlbach, 2003). It could be that a similar trend exists along the coast within *M.k. kennicottii*. A comparative study on size would have to be conducted to support this theory. To date, none of the morphometric comparisons amongst Western Screech-Owls has included measurements from birds inhabiting the north coast of British Columbia (the northern most limit of the Western Screech-Owl range in North America).

Another possible explanation for why frequencies were lower in northern Vancouver Island and the south-central mainland of B.C. compared to southern Vancouver Island could be due to larger distances between individuals (lower frequencies travel farther) (Tubaro and Segura, 1994). Low-pitched calls have long wavelengths that are more effective at penetrating vegetation, and thus carrying farther than are high-pitched sounds (Johnsgard, 1988). Estimated average distance between closest known territories in southern Vancouver Island were 1.33 km ($n = 11$ sites), 2.72 km ($n = 8$) for northern Vancouver Island, and 3.83 km ($n = 10$) between south-central B.C. territories (Appendix 1). There appears to be a greater distances between territories in south-central B.C. where suitable nesting habitat is considered limited (Fraser *et al.*, 1999). However, this could relate back to size, with larger birds occupying larger territories, resulting in greater distances between birds. Caution must be applied to interpretation of these values as an exhaustive search for all active territories was not performed.

Reproductive isolation is another possibility that may explain the observed regional variation in call structure. Obvious ecological barriers to mixing exist between the two subspecies, with the Cascade Mountains and a large water body (Georgia Strait) separating *M.k. macfarlanei* from *M.k. kennicottii* populations on Vancouver Island. In addition, Western Screech-Owls breed within very different ecosystem types in the interior than on the coast. Ecological barriers between northern and southern Vancouver Island are not as obvious. There are a number of large mountains on Vancouver Island, but the eastern and western coastlines likely provide easy access for dispersal throughout Vancouver Island. The cline in frequency characteristics of Western Screech-Owl territorial calls from southeast-to-northwest on the island may be a result of short dispersal distances from core populations.

Sharp breaks do not always exist among dialects, with grades and continuous variation blending regional accents or dialects (Baptista, 2000). Variation between island populations is clearest when the two furthest populations are compared, but changes appear to be continuous along the southeast/northwest cline. As juvenile dispersal distance appears to be limited (a mean of 14.7 km based on data from 13 females, and 5.1 km from 15 males) (Ellsworth and Belthoff, 1997; Belthoff and Dufty, 1997), this would lend support to the notion that reproductive interchange between neighbouring areas may occur, but reproductive mixing between opposing poles of the clines may be less likely. Less mixing between opposing poles of the cline may explain why territorial call structure from southern Vancouver Island is distinct from the northern Vancouver Island population sampled in this study.

Literature regarding ontogeny of vocalizations in Western Screech-Owls and birds of prey in general is limited. Cannings and Angell (2001) documented that young birds give begging whinny calls until 5-6 mo of age, and that small groups of birds, likely family groups, give territorial ('bouncing ball') and double trill calls by late summer (August-September) (Cannings and Angell, 2001). Unless determined otherwise, it can only be assumed that calls are inherited and that vocalizations are present prior to dispersal. If birds inherit their calls from their parents, but do not disperse far from the nest site and are non-migratory, neighbouring microgeographic populations are likely to overlap in call measures.

Geographic variation in bird vocalizations has important implications for many aspects of the ecology of bird populations, yet there is no generally accepted explanation of the mechanisms maintaining local dialects, or of their functional significance (Latruffe *et al.*,

2000). Considering that variation in calls is one of the primary features used to determine taxonomy of Screech-Owls, it is important to assess what truly constitutes a dialect, and whether or not there is genetic variation to support call variation. The findings of my research indicate that it is a worthwhile exercise to determine whether geographic variation in call structure is present in non-passerines, and to investigate what factors might explain the observed variation.

4.0 GENERAL DISCUSSION

4.1 The Role of Bioacoustic Research in the Conservation of Western Screech-Owls

The addition of vocal individuality to current inventory and monitoring methods for Western Screech-Owls can provide a useful tool for conservation efforts and is, in my opinion, presently underused. Few studies to date have gone past the initial step of demonstrating that individuality occurs for a given avian species, to using individuality as a monitoring tool (McGregor *et al.* 2000). Of direct application to species conservation is the understanding of turnover rates within a given population, which could provide information on population trends, and reflect habitat quality and availability.

Vocal individuality showed merit in providing a potential tool for identifying turnover rates and long-term monitoring of population trends for Western Screech-Owls on southern Vancouver Island. Relatively few studies have monitored the annual turnover of territorial owners using vocal individuality (Eakle *et al.*, 1989; Gilbert *et al.*, 1994; Peake *et al.*, 1998). Galeotti and Sacchi (2001) monitored adult, male Scops Owls over two breeding seasons, and observed that a different male defended 55-78% of territories censused in the first year, which they considered to be a high turnover rate. Initial investigation of turnover rates from this study, using a discriminant model for a southern Vancouver Island population of Western Screech-Owls, indicated a 28-64% turnover. Determination of turnover rates is dependent on accurate classification of individuals both within and between years.

Based on comparison of vocalizations between years (see Chapter 2), it may prove helpful to include the double trill call in future analyses, as a secondary confirmation of individual identification (*i.e.*, two call types to corroborate that it was the same bird between years). It

would be useful to determine whether the double trill call performs at an equal or higher correct classification than the territorial call, thus providing additional detail with which to maximize long-term monitoring of this species. It would be worthwhile to assess this method for future long-term monitoring of Western Screech-Owls.

4.1.1 Application of Vocal Individuality to Western Screech-Owl Monitoring

If vocal individuality is to become widely accepted and applied by field biologists for monitoring owls, researchers must provide realistic, and simplified where possible, guidelines. Future analyses of the primary territorial call of Western Screech-Owls in British Columbia will not require the same level of detailed measurements completed in this primary investigation of vocal individuality presented here. For example, results indicated that it was not necessary to include four note length measurements (N1-N4), or the mean frequency of the second to last note (F2), as they provided little additional discriminant ability in the classification model. Removal of these variables could reduce the time to complete spectrographic measurement procedures by approximately 30% (12 instead of 17 variables to measure). If conducting dialect studies, however, these variables appear to be stable within a given population, and should therefore be included in all analyses.

Results also indicated that a single recording session per territory was sufficient to identify one owl from another within a given breeding season. For future censusing purposes, this knowledge will save valuable field time (*i.e.*, instead of having to return to the same site to collect multiple recordings, more sites can be added to the sample size). If the goal is to determine whether the same individual occupied the same site throughout the breeding season, then multiple recordings are still necessary.

In addition to the uses outlined in this thesis, a number of other behavioural or reproductive traits can be deduced from components of vocal behaviour. Vocal monitoring can be applied to measure breeding attempts, by using the cessation of nocturnal calling as an indicator that a mate had been attracted (Tyler and Green, 1996). Herting and Belthoff (1997) used individual vocalizations of male Western Screech-Owls as a measure of aggression in their hormone/drug treatment study by recording the bird's response to tape-recorded conspecific vocalizations. Peake (1997) found that song rates in Corncrakes (*Crex crex*) monitored through vocal behaviour alone showed indications of differences in male quality resulting in differences in reproductive success. Recently, Holschuh (2004) demonstrated that call rates of Northern Saw-whet Owls in the Queen Charlotte Islands (Haida Gwaii) of B.C. could be used as an indirect indicator of a bird's condition and the quality of the habitat they occupied. Similar applications are possible with vocal behaviour in Western Screech-Owls. For example, future research on populations in B.C. could compare vocal output among birds with territories that vary in the degree of urban encroachment.

4.2 Use of Discriminant Function Analysis in Avian Bioacoustics

Initial attempts to classify individual birds using avian bioacoustics consisted of qualitative comparisons of printed spectrograms of calls, where subjects matched calls by similar visible features. In general, results of visual assessments were found to be influenced by the experience of the observer (*i.e.*, familiarity with focal species, and song/call analysis software). Recognized limitations of this technique have included observer bias, and inconsistent classification results (Terry *et al.*, 2001). Due to limitations associated with visual assessments, alternate, quantitative analyses were explored in greater detail. One of

the most widely applied quantitative methods used in studies of vocal individuality is the stepwise discriminant function analysis (DFA).

Use of the DFA to classify individuals according to the selected input variables performed well in my study. A general lack of model cross-validation (using distinct learning sets to build the model, then using this to classify independent test sets) has been considered a weak point in previous vocal individuality DFA analyses, where examples used to build the model were the same as those used to test it (Terry *et al.*, 2001). A more conservative approach to testing the accuracy of the model (percent of examples correctly classified to origin of sample) is to utilize approximately two-thirds of the data to build the model and leave one-third to test the model (Manly, 1994; Terry *et al.*, 2001; StatSoft, 2002). While this often lowers the percentage of individuals with correctly classified calls, the cross-validation provides for a more robust assessment of the model's discriminant ability.

Other techniques for classifying individual birds have included cross-correlation (Gaunt *et al.*, 1994), and neural networks (May, 1998), but DFA appears to be the most widely applied and accepted for avian vocal individuality research. Cross-correlation (which uses sound analysis software to correlate two overlapping sonograms) suffers dramatically if there are differences in background noises among the two recordings being analysed. Neural networks (complex mathematical probability-of-inclusion models, which form the basis of voice recognition software) may provide a significant advance in this field in real-time confirmation of identity (Terry *et al.*, 2001), but as yet are largely unavailable for field biology and extremely expensive to develop. At present, DFA analysis is still the most powerful tool available for this field.

It is my belief, that in addition to quantitative methods, qualitative assessments still merit use in bioacoustic research. As long as one is aware of the limitations associated with the technique, the addition of a qualitative spectrogram assessment may provide a useful confirmation of quantitative re-identification. This method may prove especially useful in the case of ambiguous classifications, as applied by Galeotti and Sacchi (2001) for between year comparisons.

4.2.2 Variables Significant within Discriminant Function Analyses

Variables that were important in classifying territorial calls to the individual of origin in the vocal individuality DFA, were not the same variables important in the DFA's conducted to distinguish between macro- and microgeographic regions. Variables that appeared to explain the greatest variation amongst individuals (vocal individuality) included: length of call (D1), internote distance measurements (D2-D7), notes per call (R1), ratio of internote measurements D3 and D6 (R2), and notes per second (R3). In contrast, at the regional scale, three frequency variables (F1, F2, and F3) showed the greatest discriminant ability at distinguishing between individuals from the three regions examined. In other words, the variables that showed little variation between individuals in an area were the vocal characteristics that remained stable within a population; it is these variables that accounted for the greatest variability between regions. Likewise, Cavanagh and Ritchison (1987) found that temporal traits were generally more variable than frequency traits for the "whinny" (primary territorial call) of Eastern Screech-Owls. Identifying stable vocal characteristics within a population is essential for comparisons between populations, while those that vary within populations are likely to provide the most cues about individuality.

4.3 Taxonomic Implications of Regional Dialects and Vocal Individuality

Vocalizations are important to the taxonomic classification of many avian species, especially non-passerines that are generally considered to inherit their vocal structure rather than learn it ('stable' characteristic for classification) (Konig *et al.*, 1999). According to Konig *et al.* (1999), vocalizations are the most important interspecific isolating mechanisms in owls, thus, different vocal patterns are an important characteristic for distinguishing taxa, especially difficult species groups such as *Glaucidium*, *Otus*, and *Megascops* (Konig *et al.*, 1999). For example, separation of the Western Screech-Owl from the Whiskered Screech-Owl (*Megascops trichopsis*) in the field is only feasible by voice (Johnsgard, 1988). Based on the importance of vocal characteristics in taxonomy of *Megascops* and other members of this phylogenetic group, it is essential to develop an understanding of regional and individual variation in those species.

Within North America, nine subspecies of Western Screech-Owl are presently recognized, based largely on morphology and vocalizations (Gehlbach, 2003), two of which are present in British Columbia, Canada. Prior to 2001, however, three subspecies were recognized in B.C. by the Ministry of Water, Land and Air Protection (formerly the Ministry of Environment) Conservation Data Centre. The three subspecies included: *M.k. kennicottii* in wet coastal forests; *M.k. saturatus* in dry coastal forests of southeastern Vancouver Island, Puget Sound and the Gulf Islands; and *M.k. macfarlanei* in the southern interior (Hekstra, 1982). A taxonomic re-evaluation resulted in merging *M.k. saturatus* back with the *M.k. kennicottii* subspecies due to lack of evidence supporting separate subspecies status (Cannings and Angell, 2001; Gehlbach, 2003) (Section 1.4).

My results indicated a high correct classification (>85%) of calls to individuals (vocal individuality), as well as individuals to their region of origin (dialects). Regional analysis of variation in the call structure of the two recognized subspecies indicates that the south-central mainland population of B.C. (*M.k. macfarlanei*) is vocally distinct from the Vancouver Island coastal population (*M.k. kennicottii*) (see Chapter 3). Also of significance, results indicated that birds occupying southern Vancouver Island (previously recognized as *M.k. saturatus*) had unique vocal characteristics from birds sampled on northern Vancouver Island. However, the difference seen at polar extremes of the distribution appear to reflect continuous change along the population gradient of the island, and thus does not necessarily indicate the need for the southern island population to be re-established as a separate subspecies. It does, however, lend support to current conservation assessments that recommend close monitoring of the southern population, as this group is suspected to be in decline due to loss of habitat and predation by Barred Owls (Chaundy-Smart, 2002; Conservation Data Centre of B.C., 2004). Loss of this population, although not necessarily representing extinction of a distinct subspecies, may constitute loss of distinct genetic diversity within the coastal population.

Overall, my results suggest that inclusion of regional variation in call structure may assist taxonomic classification of *Megascops kennicottii* in North America. It is important, however, to confirm that recognized vocal variations between subspecies are due to regional differences, not individual differences. A series of analyses could be conducted to compare samples of territorial call recordings from the nine subspecies currently recognized in North America. Regional variation amongst the North American subspecies would likely parallel the north/south cline in morphometrics, with the largest birds in the north having calls with

lower frequencies, and the smaller birds in the south having calls with higher frequencies overall. Future work should consider genetic analysis of these same populations to determine whether variation in either microsatellite or mitochondrial DNA follows the same patterns of divergence across recognised subspecies, and clinal change within the Vancouver Island subspecies, indicated by call variation. If call structure coincides with differences in genetic structure of populations, it would lend support to the use of call variation as a tool for assisting in the taxonomy of Western Screech-Owl subspecies in North America.

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Appendix 1: Western Screech-Owl survey areas and site ID's recorded between 2001-2003 on Vancouver Island and the south south-central mainland of British Columbia.

* indicates control sites for between-year analysis in Chapter 2. An X for year recorded indicates that a high quality recording was obtained that year. Only sites that were successfully recorded and used in the analysis are included in the table, which is why some of the Site ID numbering is not in sequence. The Site ID was assigned during field surveys as new territories were located, but did not always result in a successful recording.

General Area	Site Name	Site ID	Ch. 2 Vocal ID	Ch. 2 Between Year Analysis	Ch. 3 Region ID	Ch.3 Sub-Region ID	Year Recorded			Distance to nearest known territory (km)
							2001	2002	2003	
<i>Region 1 (southern Vancouver Island)</i>										
Duncan	Genoa Bay	D-1	1	1		B-1		X	X	3.37
Duncan	Mays South	D-2	2	2		B-2		X	X	2.21
Duncan	VanEeuwin	D-3	3	3		B-3	X	X	X	2.02
Duncan	Maple Bay	D-4	4	4		B-4	X	X	X	1.12
Duncan	Rigby - Mountain Rd. #1	D-5	5	5		B-5		X	X	2.15
Duncan	Mountain Road #2 - Clearcut	D-6	6	*6		B-6		X		2.15
Duncan	Mountain Road #3 - Original	D-7	7	7		B-7		X	X	2.39
Duncan	Jackson Valley Road	D-8	8	8		B-8		X	X	2.55
Duncan	Boundary Bird (Herd Rd.)	D-9	9	9		B-9	X		X	1.12
Nanaimo	Panther Lake	NAN-1	10	*10			X			>30.00
Victoria	Hazlitt Creek	V-1	16	*16	1-1	A-1		X		0.90
Victoria	Humpback Road	V-2	17	17	1-2	A-2		X	X	8.00
Victoria	Martlett Road (Sage Res.)	V-3	18	18	1-3	A-3		X	X	0.90
Victoria	Stewart Mtn. Road	V-4	19		1-4	A-4		X		1.43
Victoria	Stevens Road	V-5	20	20	1-5	A-5		X	X	3.28
Victoria	Munns Road (3836) (Tank Bird)	V-6	21	21	1-6	A-6	X	X	X	1.10
Victoria	Millstream Lake Rd. (Kennedy Res.)	V-7	22	22	1-7	A-7		X	X	1.66
Victoria	Lone Tree Road	V-8	23	*23	1-8	A-8		X		1.10
Victoria	Stag Lake Road	V-10	24	24	1-9	A-9	X	X	X	1.00
Victoria	Thomson/Mt. Newton Road	V-11	25	*25	1-10	A-10			X	8.42
Victoria	Taylor Property (Munns Road)	V-12	26		1-11	A-11	X			1.00
Victoria	Firehall Bird	V-14	27	*27	1-12	A-12	X			1.10
Victoria	Highland Estates Phase 3	V-15	28	*28	1-13	A-13			X	1.21

General Area	Site Name	Site ID	Ch. 2 Vocal ID	Ch. 2 Between Years	Ch. 3 Region ID	Ch.3 Sub- Region ID	Year Recorded			Distance to nearest known territory (km)
							2001	2002	2003	
<i>Region 2 (northern Vancouver Island)</i>										
Nimpkish Valley	Vernon Lake Campsite	NVI-1			2-1	D-1			X	2.25
Nimpkish Valley	Patway Road (East Vernon Lake)	NVI-2			2-2	D-2			X	1.84
Nimpkish Valley	Vernon Reload/Vernon Lake Road	NVI-3			2-3	D-3			X	2.61
Nimpkish Valley	Vernon Lake South	NVI-4			2-4	D-4			X	2.30
Nimpkish Valley	Woss Lake Campsite	NVI-5			2-5	D-5			X	1.36
Nimpkish Valley	Sutton Road off of Nimpkish ML	NVI-7			2-6	D-6			X	1.13
Nimpkish Valley	Atluck Lake	NVI-8			2-7	D-7			X	6.14
Nimpkish Valley	Keogh Mainline (Port McNeil)	NVI-9			2-8	D-8			X	>30.00
Nimpkish Valley	Iron Mine Transect	NVI-10			2-9	D-9			X	6.14
<i>Region 3 (south-central mainland)</i>										
Okanagan Valley	Thomas Ranch	O-1			3-1			X		2.67
Okanagan Valley	McLean Creek	O-3			3-2			X		2.67
Okanagan Valley	Park Rill Creek #3	O-4			3-3			X		1.91
Okanagan Valley	Atsiklak	O-6			3-4			X		3.98
Okanagan Valley	Bellevue	O-7			3-5			X		3.94
Okanagan Valley	Inkameep	O-8			3-6			X		8.90
Okanagan Valley	Marsh (Kelowna)	O-9			3-7			X		2.70
Okanagan Valley	Test Orchard Road	O-12			3-8			X		6.00
Okanagan Valley	Willowbrook/Cattleguard	O-13			3-9			X		1.57
Okanagan Valley	Wolfcub	O-14			3-10			X		3.98
<i>Other Areas (central Vancouver Island)</i>										
Campbell River	Beaver Lodge	C-1						X		5.64
Campbell River	Brewster Lake	C-2	11	*11		C-2		X	X	3.95
Campbell River	Quinsam River/Airport Main	C-3	12	*12		C-3		X		5.64
Campbell River	Strathcona Dam (Telemetry)	C-4	13	*13		C-4		X	X	4.65
Campbell River	Paterson Lake (Telemetry)	C-6	14	*14		C-6			X	2.26
Campbell River	Menzies Main/North Main	C-7	15	*15		C-7			X	2.26
TOTAL Sites Used in Analysis		48	28	26	32	36	8	31	29	